TWO NEW MEMBERS OF A SEX-LINKED MULTIPLE (SEXTUPLE) ALLELOMORPH SYSTEM

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INTRODUCTION

Two new eye colors have appeared in my cultures of *Drosophila ampelophila*. Both mutations show sex-linked inheritance and are of more than ordinary interest since their genes are new members of a complex multiple allelomorph system which up to this time has consisted of the three recessive mutant eye colors, white, eosin, cherry, and their dominant allelomorph of the wild fly.

MORGAN and his students have postulated that the genes for the sex-linked mutations, white eyes, eosin eyes, and cherry eyes, lie at the same locus on the X chromosome. In support of this view the evidence is advanced that the three mutants show no crossing over with each other. Moreover all three mutants show the same crossover value with any other sex-linked mutant. The numerical data in so far as it bears on the localization of the genes may be interpreted in two different ways: (1) That the material particles which bear the characters from generation to generation are arranged on the X chromosome in a linear series and that the genes for white eyes, for eosin eyes and for cherry eyes are very close together, possibly in juxtaposition. (2) That the gene upon which the red of the wild fly depends has changed in at least three different (independent) ways, giving rise respectively to white eyes, eosin eyes and cherry eyes.

The second view is preferable since it will account for the fact that a new color is produced in the F_1 when any two of these forms are hybridized. This is contrary to expectation on the first view; for if these factors lie at different loci on the X chromosome, then on crossing some of the mutant members of this system, red-eyed females of the wild type should be produced. In the female the two X chromosomes are both present and if the mutants are expressions of changes that have taken place at different levels in the chromosome then each chromosome would supply the normal allelomorph to the missing or changed gene in the other chromosome and normal conditions would be restored, that is, red-eyed females would be produced. But such is not the case.

Granted on the first view that the genes are arranged serially and closely linked, it seems not improbable that in the female, where the different members are compounded and the possibility of the interchange of materials is known to take place, that occasionally a break between the genes in question should occur with the production of a so-called crossover class. But in thousands of cases in which this particular crossover has been looked for no such individual has been found. In short the evidence goes to show that the red eye of the wild fly is affected by a unit of some kind lying at a definite locus on the X chromosome and that the unit has mutated in five different ways giving rise to white, eosin, cherry, tinged and blood.

PART I. ON THE ORIGIN, DESCRIPTION AND INHERITANCE OF TWO NEW SEX-LINKED EYE MUTANTS

1. ORIGIN AND DESCRIPTION OF THE TWO NEW SEX-LINKED EYE MUTATIONS

a. *Origin and description of blood*

"Blood" first appeared July 10, 1914, in a culture of wild stock. The parent stock originally came from Seattle, Washington, and had been in captivity for about one year. The culture had been examined many times but up to this time no unusual forms had been found. It is highly probable, however, that the original mutant had been overlooked since seven males made their appearance almost simultaneously in the stock bottle. This stock with about thirty others from different localities had been kept in a refrigerator for some time and it might be supposed that the reduced temperature was responsible for the mutation, but subsequent experiments have shown that reduced temperatures are not potent in the production of mutants.

The new eye is a dark red corresponding in color to a blood stain as made on white absorbent paper by blood rich in hemoglobin. In fact the color corresponds to next to the highest color on the hemoglobin scale as devised by TALLQUIST. The metallic fleck so apparent in the eye of the wild fly is relatively inconspicuous. As the fly ages the eye darkens somewhat and the metallic fleck disappears. When the flies are first hatched and for some time after, the eyes are somewhat translucent. The eye has the least margin of light around the border suggesting that the red has retreated from the surface. These observations were made many times during the winter of 1914-15. The cultures at this time

were kept at living-room temperature. The temperature at night however dropped much lower. Under such conditions the hatching period is about twenty-five days. I dwell on this since it may give the key to a peculiar fact about this color which will be discussed later.

When the fly first appeared it had very light eyes, despite the fact that it had been kept in an ice-box. The temperature in this box however during very hot summer weather was not so cold on the average as the living-room temperature during the winter. The temperature in the chest was probably never lower than 19° C and at times was higher. During the summer of 1915 my cultures of blood had very light eyes. Some of the bottles during the hot days of July completed development in about eight days and to my surprise the eyes of these flies were almost white. They darken with age to almost the characteristic blood. It would seem from this that the temperature has something to do with the color of the eye as it appears at the time of hatching. Most of the experiments recorded in this paper were carried out during the cool weather and the eye color remained practically constant during this time.

I have spared no pains in order to determine whether or not this mutant is identical with any of those described by MORGAN. I am absolutely certain that it is different. It is true that it resembles pink, but no confusion of the two can be made since they behave quite differently in heredity. I have reared pink for more than three years.

The only other mutant with which blood is likely to be confused is cherry especially since their behavior in heredity and linkage relations are identical. After long study with these two forms under uniform conditions I have learned that the two are different. Both forms show a range of color due to differences in age and other conditions, but cherry does not give any such range of color as does blood. In the cherry eye the pigment has apparently retreated farther from the surface than in blood and this apparently allows the light to penetrate to a greater depth. The pigment in the blood eye seems to be uniformly distributed while in the cherry eye there is just the least hint of a clumping of pigments. The cherry eye holds its translucency longer than blood.

My students have tested my conclusions in regard to the difference between these two eye colors by breeding the flies under as nearly uniform conditions as possible and submitting both lots to me for identification. In a great many trials I have not failed to make the proper identification. The fact that there is a difference is made certain by the bicolorism that appears in the sons and daughters when blood and

cherry are crossed. Attention will be called to this phenomenon later in the paper.

b. *Origin and description of tinged*

"Tinged" is a new sex-linked mutant that arose from wild stock. On November 2, 1914, while examining some 2000 flies that had hatched from over-ripe bananas that had been kept in a large fruit jar plugged with cotton, one tinged male was found. The bananas were obtained at a fruit store where for over a year I had been accustomed to collect wild stocks but up to this time this locality had yielded no unusual forms. The jar had been in the laboratory for about two weeks when the count was made. The flies had never been exposed to ether and I can think of no causative agent in connection with the origin of this mutation. Experience has taught that mutations are rare phenomena and until they can be produced experimentally on a large scale it seems almost futile to speculate on the origin of this fly. It is highly probable that this was the original mutant of its kind since several bottles of the red-eyed flies were selected and inbred for a long time, but no tinged appeared.

Tinged shows only a slight amount of color. In fact it could easily pass for white if one did not have both forms to compare. There is about the same difference in color between tinged and white as there is between a red and a white corpuscle as seen under the higher powers of the microscope. The difference is real and the two classes can be separated when seen in good light on a clear white background. From the plate of sweet peas as given in PUNNETT'S Mendelism, 1913, Plate IV (opposite page 80) I infer that there is about the same difference in color as there is between a white flower and a tinged one. The tinged flower is possibly a little darker red than the fly.

Nomenclature

The mutant, white eyes, is designated by w. The dominant normal allelomorph to w is red and is designated by the letter W. Eosin is w^e, cherry is w^c, blood is w^b, while w^t designates the gene for tinged. The female is designated by XX and the male by XY.

2. BEHAVIOR OF BLOOD WHEN CROSSED TO NORMAL WILD STOCK WITH RED EYE

a. *Red ♀ by blood ♂*

When the blood males are bred to the red-eyed females all of the offspring had red eyes like the mother. There were 214 red-eyed females

and 191 red-eyed males. These, when inbred, produced in the F_2 generation the different classes in table 1. Approximately one-half of the grandsons were like the grandfather. This is the expectation in the second generation provided blood is a recessive sex-linked character.

TABLE 1

F_2 from red ♀ by blood ♂.

Number	Red ♀♀	Red ♂♂	Blood ♂♂
1	87	46	37
2	58	32	19
3	163	55	62
Total	308	133	118

b. *Blood ♀ by red ♂*

The reciprocal cross in which the blood female was mated to the red male gave 2408 red females and 2074 blood males in the F_1. All of the sons were like the mother and all of the daughters were like the father. No exceptions are recorded in a total of 4482 flies and none is expected unless some disturbing factor like non-disjunction should interfere. When these flies are inbred all four classes are realized in the ratio of 1 : 1 : 1 : 1 as the formula demands. The results are given in table 2.

TABLE 2

F_2 from blood ♀ by red ♂.

Number	Red ♀♀	Blood ♀♀	Red ♂♂	Blood ♂♂
1	81	99	70	83
1 a[1]	119	109	94	116
2	140	115	108	110
2 a	33	29	32	29
3	67	80	65	63
3 a	101	96	72	86
4	45	42	38	41
4 a	31	34	23	21
Total	617	604	502	549

[1] The numbers 1, 1 a, 1 b, etc., indicate the first, second, third, etc., broods raised from the same mother.

3. BEHAVIOR OF TINGED WHEN CROSSED TO NORMAL WILD STOCK WITH RED EYES

a. *Red ♀ by tinged ♂*

When the red-eyed female is mated to the tinged male all of the offspring, both sons (200 ±) and daughters (200 ±) have red eyes. When these are inbred the tinged eye recurs, affecting one-half of the grandsons but none of the granddaughters. The results are given in table 3.

TABLE 3

F_2 from red ♀ by tinged ♂.

Number	Red ♀♀	Red ♂♂	Tinged ♂♂
1	100	45	39
2	58	24	28
3	39	21	18
4	47	35	30
5	80	46	44
6	71	19	34
7	87	33	44
8	78	34	39
9	113	49	35
10	71	37	36
11	18	6	5
12	70	29	33
13	59	30	21
14	82	33	27
15	66	23	26
16	39	17	12
17	148	76	56
18	44	24	24
Total	1270	581	551

b. *Tinged ♀ by red ♂*

Evidence that tinged is a sex-linked character is given by the reciprocal cross in which the tinged female is mated to the red-eyed male. In the F_1 generation all of the sons (155) have tinged eyes like the mother, while all of the daughters (156) have red eyes like the father. This is the typical case of criss-cross inheritance which the case demands. In the F_2 generation all four classes are realized in equal proportions as given in table 4.

This evidence is conclusive that blood and tinged are sex-linked characters.

TABLE 4

F_2 from tinged ♀ by red ♂.

Number	Red ♀♀	Tinged ♀♀	Red ♂♂	Tinged ♂♂
1	15	14	9	13
1 a	25	29	21	41
1 b	48	31	37	40
2	53	38	49	38
2 a	83	60	77	65
3	20	30	19	25
3 a	24	29	31	34
3 b	13	21	30	29
3 c	58	61	60	44
4	37	49	37	29
4 a	68	68	78	72
5	21	22	19	14
5 a	21	17	14	14
Total	486	469	481	458

PART II. ON THE LOCUS OF THE GENE FOR THE NEW SEX-LINKED MUTANT, BLOOD

I. LINKAGE OF BLOOD AND WHITE

When the white female is mated to the blood male the expectation is that all of the sons (501) will have white eyes like the mother and all of the daughters (468) will be white-blood compounds. In a total of 969 no red-eyed flies appeared. The F_1 were inbred with the result that all four classes appeared in the next generation, as given in tables 5, 6 and 7.

TABLE 5

F_2 from white ♀ by blood ♂.

Number	White ♀♀	White-blood compound ♀♀	White ♂♂	Blood ♂♂
1	101	92	96	91
1a	74	60	68	72
1b	44	35	55	41
2	78	76	76	78
2a	79	77	89	71
2b	13	11	11	12
3	89	93	82	90
3a	86	71	69	73
3b	30	32	20	19
4	83	91	77	83
4a	53	51	73	58
4b	17	14	18	12
5	88	102	96	94
5a	29	60	62	43
Total	864	865	892	837

TABLE 6

F_2 from white ♀ by blood ♂.

Number	First bottles				Second bottles			
	White ♀♀	White-blood compound ♀♀	White ♂♂	Blood ♂♂	White ♀♀	White-blood compound ♀♀	White ♂♂	Blood ♂♂
1	49	58	58	53	19	14	11	15
2	23	16	22	38	16	8	14	15
3	4	6	2	0	0	0	0	0
4	8	11	18	10	5	2	2	3
5	40	54	38	41	20	13	10	14
6	26	28	35	24	10	10	8	11
7	26	32	29	15	17	15	8	14
8	24	29	32	26	20	15	17	12
9	15	21	19	20	11	15	18	9
10	29	30	36	38	21	15	11	20
11	42	28	32	26	12	18	5	18
12	66	80	99	85	39	40	28	31
13	89	72	101	84	27	24	14	11
14	101	100	92	92	80	77	69	74
15	132	113	113	103	25	22	17	16
16	98	119	109	124	52	41	29	41
17	95	116	106	90	96	106	106	81
18	126	107	129	112	68	80	50	65
19					27	36	30	36
20					24	33	27	35
21					17	17	22	12
Total	993	1020	1070	981	606	601	496	533

TABLE 7

F_2 from white ♀ by blood ♂.

Number	Number of mothers	Number of fathers	First bottles				Second bottles			
			White-blood compound ♀♀	White ♀♀	Blood ♂♂	White ♂♂	White-blood compound ♀♀	White ♀♀	Blood ♂♂	White ♂♂
1	2	2	43	36	31	33	39	27	32	38
2	4	4	65	65	64	50	37	37	30	30
3	4	4	52	46	31	31	32	23	30	29
4	4	4	43	42	52	36	15	19	20	17
5	—	—	—	—	—	—	39	38	28	40
6	8	8	37	38	41	33	33	24	22	28
7	8	8	77	67	57	67	22	16	12	13
8	—	—	—	—	—	—	20	12	15	20
9	—	—	—	—	—	—	0	1	3	2
10	10	10	55	44	32	43	11	9	5	12
11	22	37	73	64	41	47	25	28	15	18
Total			445	402	349	340	273	234	212	247

In the reciprocal cross, in which the white male is bred to the blood female, all of the sons (370) have blood eyes like the mother. This results from the fact that the sons inherit their one X chromosome with its gene for the character, blood, from the mother. The daughters (312) on the other hand are white-blood compounds with eyes much lighter than blood. This results from the fact that she has two X chromosomes and is a compound of two modifications of the same gene. Inbreeding the F_1 of this cross gives evidence in accordance with expectations as recorded in tables 8 and 9.

TABLE 8

F_2 from blood ♀ by white ♂.

Number	Blood and white-blood compound ♀♀	Blood ♂♂	White ♂♂
1	130	68	68
2	71	26	42
3	48	23	20
Total	249	117	130

TABLE 9

F_2 from blood ♀ by white ♂.

Number	First bottles			Second bottles		
	Blood and white-blood compound ♀♀	Blood ♂♂	White ♂♂	Blood and white-blood compound ♀♀	Blood ♂♂	White ♂♂
1	73	42	47	16	5	6
2	76	36	36	23	17	13
3	79	19	28	—	—	—
4	34	15	22	17	8	5
5	26	10	8	14	13	7
6	27	7	12	14	7	7
7	20	10	6	14	13	10
8	43	16	15	29	8	8
9	47	24	23	21	11	14
10	33	18	25	29	18	13
11	35	28	33	28	5	8
12	139	80	79	181	79	73
13	179	79	78	18	9	8
14	252	126	92	112	37	41
15	220	92	94	194	77	87
16	269	111	127	68	10	16
17	104	43	54	—	—	—
18	42	11	14	321	139	129
19	—	—	—	92	25	28
Total	1698	767	793	1181	481	473

A summary of tables 5, 6, 7, 8 and 9, gives a total of 18149 F_2's from the cross between blood and white without the appearance of a single red-eyed fly, which is in accordance with expectations on the theory of multiple allelomorphs.

a. *Bicolorism in the F_2 generation from blood ♀ by white ♂*

It is of interest to note that bicolorism results in the F_2 generation from the cross of the blood female to the white male. This condition in the female results from the compounding of w^bX and wX. The white-blood compound female is distinctly lighter than her blood brothers (w^bXY) or blood sisters (w^bw^bXX). The white in some way reacts with blood to produce a lighter color. Some of the F_2 males and females were kept under observation. The males turned somewhat darker—a characteristic of blood stock. The white-blood compound females on the other hand became but very little, if any, darker. After more than thirty days their eyes were distinctly translucent, in marked contrast to the darkened condition of the blood stock female. To put

this difference to a test I selected from a mixture of homozygous and heterozygous females 18 of the darker females of the suspected composition $w^b w^b XX$ and bred to white males wXY. This gives a crucial test, for if they are of the formula suspected, none of their children should have white eyes. As a matter of fact one in the eighteen was questioned and this yielded some white eyes. Seventeen were of the formula postulated. Thirty-two females of the suspected formula $w^b wXX$ were bred to white males and gave white offspring according to expectations. Two were questioned; one proved to be $w^b wXX$ and one $w^b w^b XX$.

2. LINKAGE OF BLOOD AND EOSIN

MORGAN and BRIDGES (1913) demonstrated that eosin lies at the same locus in the X chromosome as white. It has just been demonstrated that blood lies at the same point in the chromosome as white. The evidence which follows substantiates the expectation that eosin and blood should lie at the same locus.

The eosin female crossed to the blood male produced 109 eosin males and 141 eosin-blood compound females. These when inbred produced in the next generation the classes as given in table 10. There are no reds in a total of 7297.

TABLE 10

F_2 from eosin ♀ by blood ♂.

Number	Number of mothers	Number of fathers	First bottles			Second bottles		
			Eosin and eosin-blood compound ♀♀	Eosin ♂♂	Blood ♂♂	Eosin and eosin-blood compound ♀♀	Eosin ♂♂	Blood ♂♂
2	6	6	143	65	62	271	129	127
3	6	6	185	39	37	140	79	104
4	6	6	91	47	51	147	67	71
5	6	6	78	45	60	194	89	112
6	5	5	103	50	47	133	60	57
7	5	5	152	62	63	139	50	61
8	5	5	133	78	61	161	38	65
9	5	5	117	60	52	139	43	47
10	5	5	142	42	47	334	81	98
11	11	4	147	73	84	268	107	125
12	17	15	154	67	79	59	22	19
13	23	12	167	67	76	100	44	38
14	10	8	100	62	59	139	52	51
Total			1712	757	778	2224	861	965

In the reciprocal cross in which the eosin male is crossed to the blood female there were 89 blood sons and 111 eosin-blood compound daughters. These inbred produced in the F_2 the classes as given in table 11. There were no red flies in either the F_1 or F_2.

TABLE 11

F_2 from blood ♀ by eosin ♂.

Number	Blood and eosin-blood compound ♀♀	Blood ♂♂	Eosin ♂♂
1	204	56	87
2	149	61	77
3	38	13	18
Total	391	130	182

The eyes of eosin stock males are about half as dark as the female. The stock breeds true to this condition. If blood lies at a different point in the chromosome than eosin it follows that red females are expected among the children of the cross. But no red daughters were found. In order to test the possibility of a break occurring between eosin and blood (which is the expectation if they lie at different levels on the chromosome) 8000 F_2's as recorded in tables 10 and 11 have been produced and not a single red-eyed fly has appeared.

The eosin-blood compound female ($w^e w^b XX$) is lighter than blood ($w^b w^b XX$) but darker than the eosin female ($w^e w^e XX$). I have classified the blood and eosin-blood compounds together in tables 10 and 11 to save labor. They can with some difficulty be separated. I have been able to separate them in cultures two weeks old, showing that the difference holds for some time. In table 11, $w^e w^b XX$ is lighter than $w^b w^b XX$ but darker than $w^e XY$.

a. *A bicolored mosaic female with two male eyes*

A mosaic female appeared in the F_1 of a cross between the blood female and eosin male, that is of unusual interest in a consideration of the effects of bicolorism that result from compounds. This female was genotypically an eosin-blood compound of the formula $w^e w^b XX$. Females of this composition normally have eyes lighter than blood but darker than eosin of the eosin female. This female differed from her sisters (500 ±) in that her right eye was typically blood and her left eye was

eosin, typical of the eosin male. In short she was a mosaic with two male eyes, one w^eX and one w^bX. The contrast between the two colors was marked and interest in the case is heightened by the fact that the eye of the eosin male is much lighter than that of the eosin female.

By way of explanation it is probable that an egg (w^bX) from the blood female was fertilized by sperm (w^eX) from the eosin male. The presence of two X's determined femaleness and with w^e and w^b present the eosin-blood compound should have resulted, as it did in all the sisters. If it be assumed that in the development of the fertilized egg the X chromosomes became separated (somatic reduction) in the cells that went to form the right and left eye, carrying with them w^b and w^e respectively, then each eye would show the color which we know they do give when they occur singly in the males. This case would seem to show that eye color is determined by the material carried to the eye by the chromosome complex and not by some secretion given off by the sex glands. In other words the bicolorism is not a direct result of compounding the allelomorphs in the female. It is not due to femaleness as such. The bicolorism is an indirect result in the sense that in the female two X chromosomes are present and consequently the two modifications of the same gene are carried to the eye where the complex asserts itself (HYDE and POWELL 1916).

3. LINKAGE OF BLOOD AND CHERRY

All the evidence shows that cherry lies at the same point in the chromosome as white, and since blood lies at the same point as white the inference is that blood and cherry are at the same locus.

The cherry female mated to the blood male produced in the F_1, 156 cherry males and 156 cherry-blood compound females. The fact that no red-eyed females were obtained, is consistent with expectations. The cherry-blood compound female eye is practically indistinguishable from the eye of the cherry male. This was verified in flies at different ages and in several crosses.

On inbreeding the F_1 no red-eyed flies are produced, but a relation comes to light which shows beyond a doubt that cherry and blood are different mutants. The males are separable into a lighter and a darker class corresponding to cherry and blood (table 12). I interpret this to mean that cherry and blood are different mutants, for if they are identical no such difference would result. Cherry and cherry-blood compound females cannot with certainty be separated.

TABLE 12

F_2 from cherry ♀ by blood ♂.

Number	Cherry and blood-cherry compound ♀♀	Cherry ♂♂	Blood ♂♂
1	50	20	22
1 a	38	26	16
1 b	34	20	13
1 c	60	39	30
1 d	44	25	19
2	16	0	9
2 a	96	22	26
2 b	74	32	42
2 c	82	80	27
2 d	77	43	31
3	40	12	16
3 a	36	27	26
3 b	23	8	6
3 c	21	13	5
4	68	43	31
4 a	50	47	20
4 b	57	31	27
4 c	44	22	24
5	8	0	2
5 a	57	33	27
5 b	96	54	52
5 c	37	23	18
5 d	33	30	10
6	254	127	109
Total	1395	777	608

The foregoing conclusion is borne out by the reciprocal cross in which the blood female is crossed to the cherry male. The sons (166) are darker than the daughters (242). The males are blood like their mother while the females are compounds. These when inbred produced the four different classes as given in table 13 without the appearance of a red-eyed fly.

These facts show that despite the fact that there is a close resemblance between blood and cherry they are different mutants and that cherry is a lighter color than blood.

TABLE 13

F_2 from blood ♀ by cherry ♂.

Number	Blood ♀♀	Cherry-blood compound ♀♀	Blood ♂♂	Cherry ♂♂
1	17	17	19	26
1 a	21	24	20	27
1 b	23	16	14	28
1 c	34	34	25	32
1 d	30	35	31	34
2	9	9	9	5
2 a	27	26	28	28
2 b	38	28	18	34
2 c	25	13	28	30
2 d	69	55	47	54
3	33	27	19	13
3 a	13	14	11	14
3 b	4	8	8	5
3 c	38	29	31	33
4	2	2	2	3
4 a	13	13	9	9
4 b	15	23	15	22
4 c	33	33	30	26
4 d	21	16	32	17
5	3	2	1	6
5 a	9	10	8	15
5 b	9	15	6	18
5 c	12	12	6	15
5 d	15	13	16	9
6	6	7	5	3
6 a	60	55	40	58
6 b	17	22	26	38
6 c	28	33	28	28
6 d	18	17	17	16
Total	642	608	549	646

4. LINKAGE OF BLOOD AND YELLOW

Yellow is a sex-linked body color allelomorphic to gray of the wild fly. It shows close but not absolute linkage with white. If blood and white lie at the same locus in the chromosome the expectation is that they will give the same (numerical) crossover classes in crosses with

yellow. To determine the linkage, females with red eyes and yellow body color were crossed to the new stock, males with gray body color and blood eyes. In the F_1 there were 60 gray red daughters and 51 yellow red males. When these were inbred the different classes were realized as given in tables 14 and 15.

TABLE 14

F_2 from yellow red ♀ by gray blood ♂.

Number	Females		Non-crossover males		Crossover males	
	Gray red	Yellow red	Yellow red	Gray blood	Yellow blood	Gray red
1	19	14	7	11	0	0
1 a	23	18	20	18	0	0
1 b	22	23	28	28	0	1
2	44	31	42	40	0	0
2 a	20	26	35	29	0	0
2 b	41	41	29	35	1	1
3	70	33	46	54	1	0
3 a	35	30	35	35	0	0
3 b	35	32	29	36	0	1
4	30	19	20	15	0	0
4 a	24	20	20	22	1	0
4 b	26	25	26	18	0	1
5	44	29	20	26	0	0
5 a	43	24	28	26	0	1
5 b	28	25	26	28	1	0
Total	504	390	411	421	4	5

TABLE 15

F_2 from yellow red ♀ by gray blood ♂.

Number	Females		Non-crossover males		Crossover males	
	Gray red	Yellow red	Yellow red	Gray blood	Yellow blood	Gray red
1	27	23	18	32	1	2
1 a	11	5	5	11	0	0
Total	38	28	23	43	1	2

These tables show that this experiment differs in the F_2 from the results obtained in previous experiments in this paper in that crossover classes are obtained. The crossover classes, as has been explained, are

explicable on the assumption that yellow and blood lie at different levels on the chromosome. Yellow is not a member of this multiple allelomorph system, but it lies very close to it, since the crossover classes with blood are very small. There are 12 crossovers in a total of 910 males. The ratio of the crossovers to the total number of males gives the crossover value of 1.3. This is interpreted to mean that yellow lies at 1.3 units from the point under investigation. Yellow has been shown to be the farthest point at the left end of the X chromosome. Its locus is designated zero. We infer that blood lies at 1.3 to the right of yellow. These numbers are too small upon which to base a very accurate measurement but they correspond with the crossover value 1.1, which has been obtained between yellow and white.

Evidence on the linkage between blood and yellow is given by the reciprocal cross in which the gray blood female and the yellow red male were used as the parents. In the F_1 there were 197 gray red daughters and 164 gray blood sons. On inbreeding these flies there appeared in the F_2 a total of 3851 males of which 108 belonged to the crossover classes. This gives a crossover value of 2.80 which is somewhat higher than in the previous cross. Detailed counts are recorded in tables 16, 17 and 18. In the first series of bottles (table 16) there are 1885 males, 57 of which are crossovers, a crossover value of 3.02. In the second series (table 17) from the same parents the crossover value is 3.32. In the third series (table 18) of bottles from the same parents the crossover value is 2.45. The evidence from this is not conclusive that crossing over between characters in the X chromosome may change with age. In another series of experiments in which the crossing over between characters in this chromosome has been tested, no change concomitant with age has been found.

5. LINKAGE OF BLOOD AND MINIATURE

It seemed desirable to study the linkage of blood with some mutant whose gene lies at a greater distance than does yellow from this multiple allelomorph locus. Accordingly miniature was chosen, since it has been shown to give a crossover value corresponding to its locus of 36.2 with other members of this system.

Miniature is a sex-linked wing mutation characterized by the fact that its wings extend but little beyond the tip of the abdomen. It is an excellent form to contrast with an eye color because its viability is high and the crossover classes are easily recognized.

The red miniature female crossed to the blood long male produced

TABLE 16

F_2 from gray blood ♀ by yellow red ♂ (first bottles).

Number	Females		Non-crossover males		Crossover males	
	Gray blood	Gray red	Gray blood	Yellow red	Gray red	Yellow blood
1	25	18	11	18	1	0
2	15	3	12	2	0	0
3	20	16	17	15	0	0
4	10	5	7	5	1	0
5	14	10	9	5	0	0
6	18	18	14	14	1	0
7	8	6	5	7	1	0
8	9	9	11	9	0	0
9	16	11	10	6	0	0
10	30	26	26	27	1	0
11	124	97	129	74	0	2
12	103	87	82	92	2	3
13[1]	135	117	122	75	8	4
14	117	95	106	80	0	4
15	138	96	113	69	5	1
16	164	63	123	45	3	4
17	72	54	69	35	2	0
18[2]	146	148	113	96	5	5
19	34	30	29	11	0	0
20	12	9	12	1	1	0
21	78	44	88	34	2	1
Total	1288	962	1108	720	33	24

[1] Plus one gray white male.
[2] Plus one gray white male.

TABLE 17

F_2 from gray blood ♀ by yellow red ♂ (second bottles).

Number	Females		Non-crossover males		Crossover males	
	Gray blood	Gray red	Gray blood	Yellow red	Gray red	Yellow blood
1	2	7	5	2	1	0
2	10	0	8	0	0	0
3	7	9	7	2	1	0
4	6	5	2	4	0	0
6	15	10	13	12	1	0
7	19	8	9	4	0	1
8	2	3	5	0	1	0
9	12	15	8	5	1	0
10	5	8	8	2	0	1
11	9	8	8	1	0	0
12	33	44	33	15	2	1
17	118	94	87	80	3	2
18	111	79	63	75	2	1
22	133	96	154	71	1	1
Total	482	386	410	273	13	7

in the F_1, 134 red long daughters and 104 red miniature sons. These were inbred and produced 740 crossovers in the F_2 in a total of 1964 males. This gives a crossover value of 37.6. Detailed counts are recorded in tables 19 and 20.

TABLE 18

F_2 from gray blood ♀ by yellow red ♂ (third bottles).

Number	Females		Non-crossover males		Crossover males	
	Gray blood	Gray red	Gray blood	Yellow red	Gray red	Yellow blood
11	100	86	72	51	2	4
12	77	66	67	38	1	1
13	77	42	60	49	1	1
14	104	62	90	43	2	2
16	70	52	42	38	2	0
17	104	71	103	82	2	3
19	109	71	81	56	2	1
20	103	69	82	41	2	1
21	130	136	88	39	4	0
22	67	41	40	70	0	0
Total	941	696	725	507	18	13

TABLE 19

F_2 from red miniature ♀ by blood long ♂ (first bottles).

Number	Females		Non-crossover males		Crossover males	
	Red long	Red miniature	Blood long	Red miniature	Red long	Blood miniature
1	23	23	16	21	10	5
2	14	11	7	8	3	4
3	9	11	6	6	2	10
4	13	12	8	10	7	1
5	29	16	10	16	8	9
6	33	22	20	23	11	15
7	6	11	2	10	4	0
8	15	14	9	1	2	9
9	12	15	7	3	6	3
10	16	21	13	10	4	6
12	57	59	43	49	21	9
13	109	106	42	60	28	40
14	108	127	49	62	35	38
15	115	98	52	67	36	38
16	108	101	75	47	46	38
17	8	10	3	4	2	3
18	44	50	15	34	19	13
Total	719	707	377	431	244	241

TABLE 20

F_2 from red miniature ♀ by blood long ♂ (second bottles).

Number	Females		Non-crossover males		Crossover males	
	Red long	Red miniature	Blood long	Red miniature	Red long	Blood miniature
1	13	12	8	14	6	3
2	13	9	14	2	2	4
3	15	12	7	10	3	2
4	14	8	12	5	4	1
5	11	14	4	5	4	1
6	13	16	6	7	5	5
7	7	7	3	6	3	5
8	2	9	0	9	2	1
9	8	7	9	6	2	5
10	9	17	5	7	6	3
11	5	5	2	0	5	2
12	47	38	21	30	14	11
13	47	35	4	18	19	5
14	45	72	12	33	15	15
15	86	73	34	67	39	21
16	74	49	17	31	23	19
Total	409	383	164	250	152	103

The reciprocal cross is given in tables 21 and 22 in which the red miniature male is bred to the blood long female. In the F_1 there are

TABLE 21

F_2 from blood long ♀ by red miniature ♂ (first bottles).

Number	Females		Non-crossover males		Crossover males	
	Red long	Blood long	Blood long	Red miniature	Red long	Blood miniature
1	63	33	22	44	24	16
2	33	31	13	17	12	11
3	4	4	7	3	3	1
4	26	21	17	11	11	12
5	17	16	8	18	2	8
6	21	18	12	14	4	4
7	18	18	13	9	4	7
8	35	28	19	9	16	12
9	15	17	8	8	5	9
11	94	118	54	68	25	27
12	119	137	69	73	43	46
13	52	49	22	34	19	9
14	144	120	77	88	40	37
15	61	40	47	38	20	15
16	40	50	20	27	18	17
17[3]	105	90	87	66	45	39
Total	847	790	495	527	291	270

[3] Plus one white long male.

169 red long daughters and 140 blood long sons. When these were inbred there appeared in the F_2 a total of 2799 males, 1073 of which were crossovers. This gives a crossover value of 38.3, practically the same as in the previous experiment, as is to be expected.

TABLE 22

F_2 from blood long ♀ by red miniature ♂ (second bottles).

Number	Females		Non-crossover males		Crossover males	
	Red long	Blood long	Blood long	Red miniature	Red long	Blood miniature
1	11	13	4	6	5	2
2	6	8	4	5	8	0
3	6	3	4	3	2	0
4	11	13	9	1	5	1
5	16	13	9	5	2	2
6	12	3	2	1	0	0
7	13	15	9	3	7	4
8	12	8	4	5	1	4
9	6	13	7	3	5	2
11	165	144	75	62	64	43
12	158	148	80	70	70	44
13	63	60	20	21	18	9
14	118	122	72	78	49	53
15	193	80	54	88	70	42
Total	790	643	353	351	306	206

The totals from the cross and its reciprocal give 1813 crossovers in a total of 4763 males, a percentage of 38.1. This expresses the linkage between miniature and blood. This substantiates the claim that blood lies at or very near white, since it gives the same linkage with miniature that such an hypothesis demands.

PART III. ON THE LOCUS OF THE GENE FOR THE NEW SEX-LINKED MUTANT, TINGED

1. LINKAGE OF TINGED AND WHITE

The method followed in this part of the paper in determining the linkage of tinged is practically the same as that employed in the case of blood.

When the white female is crossed to the tinged male all of the sons (494) have white eyes like the mother. This fulfills our expectations

since he receives his one X chromosome from the mother. The daughters (499) on the other hand have very light eyes representing a compound of w and w^t. This is to be expected, provided tinged is a member of the same allelomorphic system as white. When the F_1 is inbred all four classes are realized in the F_2 as given in tables 23 and 24. These

TABLE 23

F_2 from white ♀ by tinged ♂.

Number	First bottles: Flies used as mothers	First bottles: Flies used as fathers	First bottles: White and tinged-white compound ♀♀	First bottles: Tinged and white ♂♂	Second bottles: White and tinged-white compound ♀♀	Second bottles: Tinged and white ♂♂
1	1	1	23	28	—	—
4	1	1	13	20	—	—
5	1	1	29	17	—	—
8	1	1	14	19	96	111
9	1	1	18	24	—	—
10	1	1	33	37	—	—
12	1	1	37	32	—	—
13	1	1	30	38	—	—
14	5	5	127	148	—	—
15	5	5	150	110	65	69
16	3	2	24	13	52	36
17	24	1	23	21	117	106
18	5	5	52	32	69	46
19	5	5	30	24	82	60
20	5	5	36	52	47	40
21	5	5	39	27	83	63
22	5	5	73	76	51	28
23	5	5	62	69	52	38
24	5	5	80	61	60	73
Total			893	848	774	670

TABLE 24

F_2 from white ♀ by tinged ♂.

Number	Females: White	Females: White-tinged compound	Males: White	Males: Tinged
1	46	49	44	46
1a	67	53	66	73
2	25	35	34	30
2a	77	81	52	61
Total	215	218	196	210

flies occur in the ratio of 1 : 1 : 1 : 1. There are 4024 F_2's without the appearance of a single red-eyed fly.

The linkage between white and tinged was also tested by means of the reciprocal cross. The tinged female and white male were used as the parents. In the F_1 there were 105 white-tinged compound females and 75 tinged males. These when inbred produced in the next generation the classes as given in tables 25 and 26. The white and tinged males are classified in the same columns in order to facilitate counting. The different classes can however be separated and in several bottles not recorded here the white and tinged males in the F_2 from this cross do occur in practically equal numbers. The point of interest here is that in a total of 11701 F_2's from white by tinged not a single red-eyed fly appeared. Crossing over between tinged and white could not have taken place.

TABLE 25

F_2 from tinged ♀ by white ♂.

Number	Number of mothers	Number of fathers	First bottles		Second bottles	
			Tinged and tinged-white compound ♀♀	Tinged and white ♂♂	Tinged and tinged-white compound ♀♀	Tinged and white ♂♂
1	1	1	31	40	—	—
2	1	1	38	29	—	—
3	1	1	44	32	—	—
4	1	1	46	43	—	—
5	1	1	112	90	—	—
6	1	1	47	35	—	—
8	1	1	107	104	—	—
9	1	1	39	34	—	—
10	1	1	26	15	—	—
11	1	1	116	116	—	—
12	1	1	34	37	—	—
13	5	5	68	68	178	163
14	5	5	108	109	207	89
16	5	5	36	35	200	162
17	—	—	—	—	203	185
19	5	5	31	34	—	—
20	5	5	12	14	153	159
21	5	5	137	131	177	187
22	5	5	43	63	—	—
23	5	5	47	56	58	41
25	10	10	68	77	41	36
26	—	—	—	—	96	84
27	3	3	19	23	—	—
Total			1209	1185	1313	1106

2. LINKAGE OF TINGED AND EOSIN

The eosin female bred to the tinged male yielded 130 eosin-tinged compound females and 139 eosin males. The eosin-tinged compound

TABLE 26

F_2 from tinged ♀ by white ♂.

Number	Number of mothers	Number of fathers	First bottles		Second bottles	
			Tinged and tinged-white compound ♀♀	Tinged and white ♂♂	Tinged and tinged-white compound ♀♀	Tinged and white ♂♂
1					46	33
5					53	35
6					92	39
8					66	58
9					28	10
11	5	5	103	88	157	156
12	5	5	133	115	113	102
13	5	5	15	8	114	98
15					70	73
16	5	5	73	89	87	74
17	19	19	12	3	82	59
18	10	10	67	39	99	66
19	13	6	43	38	91	67
20					45	25
Total			446	380	1143	895

female is of the same color as the eosin male. Attention has already been called to the fact that the eosin male is about half as dark as the eosin female. The presence of w^t in the compound female $w^t w^e XX$ obliterates in the F_1 the sexual dimorphism that normally characterizes the eyes of the eosin stock.

TABLE 27

F_2 from eosin ♀ by tinged ♂.

Number	First bottles			Second bottles		
	Eosin and eosin-tinged compound ♀♀	Tinged ♂♂	Eosin ♂♂	Eosin and eosin-tinged compound ♀♀	Tinged ♂♂	Eosin ♂♂
1	34	10	12	68	48	30
2	137	59	64	93	20	43
3	184	78	87	75	33	60
4	119	43	31	28	9	13
5	101	32	37	121	47	50
6	106	43	65	74	27	32
7	72	31	30	25	7	13
8	48	15	33	155	56	76
9	162	45	68	178	53	63
10	0	0	0	42	37	19
12	137	45	76	69	27	37
13	98	45	56	21	26	16
14	116	54	49	12	3	8
15	34	15	24	2	1	2
16	48	20	27	47	32	34
Total	1396	535	659	1010	426	496

On inbreeding the F_1 of this cross all four classes are realized in the F_2 in equal proportions, as given in table 27. The eosin and eosin-tinged females have been classified together in order to facilitate counting. In a total of 4522 flies recorded in the F_2 of this cross not a single red-eyed fly appeared.

The reciprocal cross was also made. The tinged female was mated to the eosin male. There were 166 eosin-tinged compound daughters and 175 tinged males. The eosin-tinged compounds are a little darker than their eosin brothers, but lighter than eosin females. These flies when inbred produced in the F_2 four classes in practically equal numbers as given in table 28. In a total of 2760 F_2's no red-eyed flies were found.

TABLE 28

F_2 from tinged ♀ by eosin ♂.

Number	Females		Males	
	Tinged	Eosin-tinged compound	Tinged	Eosin
1	119	136	107	107
2	103	97	58	79
3	90	112	90	113
4	58	81	57	47
5	87	69	68	70
6	64	84	59	46
7	93	114	69	66
8	107	104	106	100
Total	721	797	614	628

TABLE 29

F_2 from cherry ♀ by tinged ♂.

Number	Females		Males	
	Cherry	Cherry-tinged compound[4]	Cherry	Tinged
1	31	28	25	29
2	37	36	36	41
Total	68	64	61	70

3. LINKAGE OF TINGED AND CHERRY

The cherry female mated to the tinged male produced in the F_1, 208 cherry-tinged compound daughters and 188 cherry males. The com-

[4] The eyes of these flies were as light as eosin males.

pound females are much lighter than their cherry brothers. In fact the cherry-tinged compound is as light as the eosin male. These flies when inbred produced in the F_2 four classes as shown in table 29. In a total of 363 F_2's no red-eyed flies were found.

The linkage between tinged and cherry was studied in the reciprocal cross. The tinged female was crossed to the cherry male. All the sons (255) have tinged eyes like the mother. The daughters (274) are cherry-tinged compounds with eyes darker than their brothers. These flies when inbred produced 1217 F_2's without the production of a single red-eyed fly, which indicates that the linkage between tinged and cherry is absolute (table 30).

TABLE 30

F_2 from tinged ♀ by cherry ♂.

Number	Females		Males	
	Tinged	Cherry-tinged compound	Tinged	Cherry
1	76	42	61	54
2	69	63	67	54
3	62	47	59	59
4	84	83	71	75
5	38	37	65	51
Total	329	272	323	293

4. LINKAGE OF TINGED AND YELLOW

The expectation is that tinged will show the same linkage relations as other members of the multiple allelomorph system when tested with yellow. The yellow red female crossed to gray tinged male gave in the F_1, 11 gray red daughters and 7 yellow red sons. These were inbred and produced in the F_2 the different classes as recorded in table 31. There are 2 crossovers in a total of 147 males, a crossover value of 1.4. The results are too small upon which to calculate a very accurate linkage value. It is evident that the crossover class is small, which indicates that the linkage between the two genes in question is very close.

TABLE 31

F_2 from yellow red ♀ by gray tinged ♂.

Females		Non-crossover males		Crossover males	
Gray red	Yellow red	Gray tinged	Yellow red	Yellow tinged	Gray red
86	66	62	83	0	2

More conclusive evidence on the linkage between tinged and yellow is given by the reciprocal cross. The gray tinged female and yellow red male were used as the parents. In the F_1 there were 100 ± red daughters and 100 ± gray tinged sons. These were inbred with the results recorded in tables 32, 33 and 34.

A summary of these tables gives a total of 2446 males, 49 of which are crossovers. This gives a linkage of 2.00 which corresponds favorably with 2.80 obtained in the cross between blood and yellow. The first bottles (table 32) give a crossover value of .86. The second bottles (table 33) from the same parents give a crossover value of 3.6. The third bottles (table 34) from the same parents give a crossover value of 2.8.

TABLE 32

F_2 from gray tinged ♀ by yellow red ♂ (first bottles).

Number	Flies used as mothers	Flies used as fathers	Females		Non-crossover males		Crossover males	
			Gray red	Gray tinged	Yellow red	Gray tinged	Gray red	Yellow tinged
1	1	1	13	7	16	17	1	0
2	1	1	7	14	10	9	0	0
3	1	1	13	9	3	6	0	0
5	1	1	10	7	7	5	0	0
6	1	1	5	10	6	8	0	0
7	1	1	5	5	1	1	0	0
10	1	1	17	15	14	12	0	0
11	1	1	15	13	9	13	0	0
12	1	1	23	22	16	13	0	0
13	1	1	15	13	6	16	0	0
14	1	1	15	17	13	19	0	0
15	1	1	11	13	16	17	0	0
16	1	1	23	16	15	12	0	1
17	5	5	16	12	5	17	0	0
18	5	5	46	34	34	43	0	0
19	5	5	33	42	25	32	1	0
20	5	5	54	55	34	43	0	0
21	5	5	27	26	13	12	0	1
22	5	5	40	26	17	31	0	0
23	5	5	45	32	18	28	0	0
24	5	5	42	35	23	32	0	0
25	5	5	57	42	28	31	0	1
26	10	10	19	18	6	18	0	0
27	10	10	18	18	14	17	0	0
28	10	10	84	73	62	61	2	1
Total			653	574	411	513	4	4

5. LINKAGE OF TINGED AND MINIATURE

The linkage between these two factors was first determined by crossing the red miniature female to the tinged long male. In the F_1 there

were 200 ± red long daughters and 200 ± red miniature sons. These when inbred produced in the F_2 a total of 6338 males, 2262 of which were crossovers. The percentage of the crossover class of the total is 35.5 which expresses the linkage between tinged and miniature. De-

TABLE 33[5]

F_2 from gray tinged ♀ by yellow red ♂ (second bottles).

Number	Females				Non-crossover males				Crossover males			
	Gray red		Gray tinged		Yellow red		Gray tinged		Gray red		Yellow tinged	
17	4	14	7	5	2	4	1	9	0	0	0	0
18	16	25	9	31	4	23	10	20	1	1	0	1
19	8	17	6	15	1	16	5	4	1	1	0	2
20	27	20	23	15	24	11	24	15	2	1	0	0
21	33	14	26	8	18	7	18	12	0	2	0	0
22	32	22	28	19	23	11	11	23	0	0	1	1
23	23	9	23	18	1	3	16	12	0	0	0	0
24	20	10	14	7	2	7	11	9	0	0	0	0
25	37	16	29	7	17	18	34	11	3	0	0	0
26	22	27	11	28	5	17	10	20	0	1	0	1
27	21	22	14	22	9	11	7	26	0	1	1	0
28	9	37	2	43	5	8	7	21	0	1	0	0
Total	252	233	192	218	111	136	154	182	7	8	2	5

TABLE 34[6]

F_2 from gray tinged ♀ by yellow red ♂ (third bottles).

Number	Females				Non-crossover males				Crossover males			
	Gray red		Gray tinged		Yellow red		Gray tinged		Gray red		Yellow tinged	
17	19	13	19	7	14	7	7	9	0	0	0	0
18	36	25	22	12	23	18	18	19	0	0	0	1
19	33	20	23	13	16	23	24	22	0	1	0	0
20	44	23	20	20	24	15	23	16	0	0	0	0
21	26	16	24	17	17	23	24	24	0	2	0	2
22	42	10	22	10	19	11	22	14	2	1	2	1
23	34	32	41	11	17	15	37	12	0	0	1	0
24	17	13	25	4	24	3	20	6	0	0	0	0
25	46	25	34	29	30	17	42	26	0	3	1	0
26	27		29		24		36		0		0	
27	29		17		10		24		0		0	
28	47	26	41	32	31	22	32	30	1	0	1	0
Total	400	203	317	155	249	154	309	178	3	7	5	4

[5] The left column under each type gives the count on April 5, the right column on April 12, from the same bottles.

[6] The left column under each type gives the first count, the right the second count from the same bottles.

tailed counts are recorded in tables 35, 36 and 37. In the first bottles (table 35) the crossover value is 35.0. In the second bottles from the same parents (table 36) the crossover value is 37.4 while in the third bottles from the same parents (table 37) the crossover value is 34.6. No change concomitant with age is evident.

The linkage between the same points in question was studied by means of the reciprocal cross in which the tinged long female was mated to the red miniature male. There were 426 red long daughters and 396 tinged long sons. These when inbred produced F_2's as given in tables

TABLE 35

F_2 from red miniature ♀ by tinged long ♂ (first bottles).

Number	Flies used as mothers	Flies used as fathers	Females		Non-crossover males		Crossover males	
			Red long	Red miniature	Tinged long	Red miniature	Red long	Tinged miniature
1	1	1	23	10	2	8	7	6
2	1	1	9	18	6	10	4	10
3	1	1	29	30	12	21	7	7
4	1	1	21	17	4	5	2	0
5	1	1	15	9	4	5	2	3
6	1	1	6	5	0	1	0	0
7	1	1	10	13	7	3	2	11
8	1	1	22	23	7	16	4	5
9	1	1	27	25	9	16	7	8
10	1	1	27	19	8	9	5	6
11	1	1	16	8	4	9	4	1
12	1	1	42	46	34	38	19	17
13	1	1	16	13	3	9	4	4
14	1	1	14	13	6	8	2	6
15	1	1	67	60	38	43	24	29
16	5	5	122	120	74	69	34	47
17	5	5	86	84	39	59	19	19
18	5	5	80	74	32	47	31	21
19	5	5	19	44	19	30	16	11
20	5	5	50	56	34	35	16	20
21	5	5	55	40	31	41	24	15
22	5	5	152	123	66	76	37	24
23	5	5	84	62	40	46	24	21
24	5	5	15	17	7	11	9	6
25	5	5	105	122	62	77	41	46
26	5	5	54	33	23	26	14	11
27	5	5	65	48	37	40	14	17
28	5	5	71	64	49	47	21	26
29	5	5	64	44	37	31	15	15
30	5	5	66	62	31	39	24	13
31	10	10	76	70	43	45	23	16
32	2	2	45	40	19	24	15	10
33	10	10	105	89	61	42	26	32
34	10	10	145	140	70	90	46	34
35	10	10	137	111	65	57	37	31
36	10	10	124	109	50	67	41	35
37	10	10	115	105	61	78	37	34
Total			2179	1966	1094	1287	667	617

TABLE 36

F_2 from red miniature ♀ by tinged long ♂ (second bottles).

Number	Females		Non-crossover males		Crossover males	
	Red long	Red miniature	Tinged long	Red miniature	Red long	Tinged miniature
16	59	32	22	18	15	9
17	29	24	16	12	10	2
18	53	15	17	4	20	2
19	65	55	29	24	22	13
20	17	35	19	8	14	5
21	48	26	27	12	9	7
22	48	43	13	11	17	6
23	57	29	25	19	16	8
24	60	58	24	40	16	19
25	52	36	19	13	15	3
26	25	22	9	5	9	3
27	39	42	15	21	20	16
28	58	36	15	18	18	9
29	41	30	17	21	11	9
31	73	71	36	43	21	18
32	13	17	11	13	9	2
33	71	45	25	14	13	11
34	74	62	25	34	26	12
35	90	103	57	49	34	31
36	103	58	39	39	27	26
37	101	81	52	53	23	26
Total	1176	920	512	471	365	237

TABLE 37

F_2 from red miniature ♀ by tinged long ♂ (third bottles).

Number	Females		Non-crossover males		Crossover males	
	Red long	Red miniature	Tinged long	Red miniature	Red long	Tinged miniature
19	57	81	35	35	22	23
21	54	40	28	30	17	12
23	70	55	37	26	22	24
24	80	55	42	33	18	20
25	55	80	30	32	19	10
31	57	46	37	32	13	12
33	57	69	25	36	11	21
34	31	23	26	9	17	7
35	101	90	38	48	23	19
36	58	42	21	20	13	11
37	62	71	32	60	19	23
Total	682	652	351	361	194	182

38, 39 and 40. Tables 41 and 42 give results obtained in a repetition of the experiment. In a total of 7153 males obtained from this cross there are 2641 crossovers, a crossover value of 37.0 which agrees with 35.5 obtained in the previous cross.

The first bottles (table 38) give a crossover value of 35.8. The second bottles from the same parents (table 39) give a crossover value of 30.1. The third bottles from the same parents (table 40) give a crossover value of 37.4. In the second experiment the first bottles (table 41) give a crossover value of 39.3 while the second bottles from the same parents (table 42) give a crossover value of 35.3. The facts in this paragraph would seem to indicate that the coupling strength remains fairly constant with age.

TABLE 38

F_2 from tinged long ♀ by red miniature ♂ (first bottles).

Number	Flies used as mothers	Flies used as fathers	Females		Non-crossover males		Crossover males	
			Red long	Tinged long	Tinged long	Red miniature	Red long	Tinged miniature
1	1	1	21	22	21	8	8	12
2	1	1	33	62	27	26	17	21
3	1	1	14	21	9	12	4	10
4	1	1	40	25	19	10	8	6
6	1	1	13	15	9	9	5	8
7	1	1	28	7	8	22	34	5
8	1	1	63	34	17	25	8	41
9	1	1	7	35	36	12	4	6
10	1	1	11	14	9	9	6	5
11	1	1	18	14	9	7	2	8
12	1	1	20	12	8	16	7	10
13	1	1	10	21	16	32	6	12
14	1	1	67	26	13	19	13	7
15	1	1	28	19	11	6	2	1
16	1	1	10	11	9	12	7	14
17	1	1	18	15	9	13	6	2
18	9	3	16	11	8	7	2	4
19	5	5	11	11	12	13	4	6
20	5	5	9	17	8	8	9	5
22	5	5	0	0	0	0	0	0
23	5	5	45	27	22	25	15	9
24	5	5	53	19	15	9	2	8
25	4	4	29	29	30	15	7	1
26	10	10	22	47	20	34	16	20
27	10	10	64	45	23	46	13	11
28	10	7	20	60	41	37	25	18
Total			670	619	409	432	230	223

The total number of F_2's from both the cross and its reciprocal gives 13491 males of which 4903 belong to the crossover classes. This gives a crossover value of 36.4. This agrees with the value 38.1 obtained between blood and miniature as is the expectation.

6. LINKAGE OF TINGED AND BAR

Bar is a sex-linked dominant mutant first described by TICE (1914).

TABLE 39

F_2 from tinged long ♀ by red miniature ♂ (second bottles).

Number	Females		Non-crossover males		Crossover males	
	Red long	Tinged long	Tinged long	Red miniature	Red long	Tinged miniature
1	38	32	16	27	11	9
2	16	44	23	1	6	10
3	29	27	13	7	16	6
4	22	14	24	12	14	9
6	54	56	16	13	29	10
8	35	42	18	27	10	6
9	29	15	14	10	8	5
10	39	30	45	28	16	25
11	66	39	25	25	16	20
12	21	18	17	18	5	15
15	39	21	13	10	8	7
16	24	23	9	2	8	2
17	50	32	30	31	17	16
18	36	11	17	11	5	13
19	15	43	23	47	23	10
20	16	17	8	14	10	9
23	36	20	15	15	5	17
24	33	51	29	6	15	5
26	76	16	9	23	14	6
28	60	27	20	10	9	9
Total	734	578	384	337	245	209

TABLE 40

F_2 from tinged long ♀ by red miniature ♂ (third bottles).

Number	Females		Non-crossover males		Crossover males	
	Red long	Tinged long	Tinged long	Red miniature	Red long	Tinged miniature
18	63	41	34	23	7	6
19	55	41	35	33	21	21
20	45	28	24	39	16	17
22	44	36	16	21	18	10
23	40	48	26	30	16	9
25	41	50	17	25	19	7
26	50	40	24	26	15	26
27	61	60	28	28	29	18
28	54	56	34	27	20	17
Total	453	400	238	252	161	131

Flies homozygous for this character have a narrow vertical streak of an eye; the ommatidia on both sides are absent. The shape of the eye in normal wild stock is hemispherical and stands out in marked contrast as compared with bar. A fact of interest is that the heterozygous flies differ in eye shape from the bar of the homozygous. Heterozygous flies

TABLE 41

F_2 from tinged long ♀ by red miniature ♂ (first bottles).

Number	No. of mothers	No. of fathers	Females		Non-crossover males		Crossover males	
			Red long	Tinged long	Tinged long	Red miniature	Red long	Tinged miniature
1	3	1	3	0	0	0	0	0
2	8	8	39	37	17	14	6	16
3	8	8	8	11	1	3	2	1
4	8	8	108	102	24	76	23	69
5	6	6	50	22	10	37	9	36
6	6	6	95	83	52	78	25	30
7	6	6	64	63	18	32	15	33
8	6	6	23	6	12	42	10	6
9	6	6	35	28	2	3	7	2
10	6	6	79	62	25	49	25	36
11	8	8	89	75	38	49	25	19
12	4	4	90	62	34	73	26	34
13	4	4	64	60	14	48	21	28
14	10	10	38	29	19	17	8	6
15	10	10	49	48	15	25	8	5
16	3	3	4	9	6	4	2	7
17	15	15	40	12	3	18	5	0
18	15	15	54	60	25	36	12	19
19	7	7	—	—	-	-	—	—
20	56	45	93	139	15	70	29	45
Total			1025	908	330	674	258	392

are characterized by the eye being irregular in shape, often kidney shaped. They can readily be separated from the homozygous flies and have been so recorded in the tables.

The red bar female crossed to the tinged normal male produced 215 heterozygous red bar daughters and 200 red bar sons. These when inbred produced the different classes as given in table 43. This table records a total of 2401 males, 1111 of which are crossovers. This is a percentage of 46.3 which expresses the crossover value between tinged and bar.

In the reciprocal cross the tinged normal female and the red bar male were used as the parents. In the F_1 there were 735 red bar daughters and 670 tinged normal sons. These when inbred produced in the next generation the different classes as given in table 44. There are 10545 males, 4672 of which belong to the crossover classes. This gives a crossover value of 44.3. Likewise there were 11113 females of which 4920 or 44.3 per cent are crossovers. The crossover value from both the

TABLE 42

F_2 from tinged long ♀ by red miniature ♂ (second bottles).

Number	Females		Non-crossover males		Crossover males	
	Red long	Tinged long	Tinged long	Red miniature	Red long	Tinged miniature
1	39	37	10	29	14	15
2	79	63	49	52	27	13
3	91	70	40	36	36	20
4	59	51	41	29	25	18
5	150	109	73	85	33	53
6	129	108	75	54	38	24
7	21	15	4	5	8	4
8	57	30	28	3	7	2
9	86	81	64	41	38	22
10	65	59	40	39	24	16
11	108	101	76	57	42	30
12	66	47	20	19	20	21
13	100	80	49	47	29	16
14	79	49	28	30	22	9
15	34	46	21	13	10	5
16	28	34	20	26	6	11
17	95	85	43	42	50	13
18	33	20	18	11	5	5
19	72	54	22	23	9	15
20	57	83	42	52	17	20
Total	1448	1222	763	693	460	332

TABLE 43

F_2 from red bar ♀ by tinged normal ♂.

Number	Females		Non-crossover males		Crossover males	
	Homozygous red bar	Heterozygous red bar	Red bar	Tinged normal	Red normal	Tinged bar
1	6	7	1	5	2	2
	31	38	22	19	12	11
	21	23	15	15	2	9
2	6	14	6	3	2	6
	46	65	28	33	26	19
	20	17	11	10	9	10
3	31	36	15	8	15	12
	28	21	10	10	8	9
	49	32	19	17	19	18
4	67	71	42	48	67	18
Total	305	324	169	168	162	114
Total[7]	977	987	470	483	421	414
Grand total	1282	1311	639	651	583	528

[7] Unpublished data from POWELL.

cross and its reciprocal is 44.4 (10703 crossovers in a total of 24059) which agrees with the crossover value between bar and white as obtained by TICE.

TABLE 44[8]

F_2 from tinged normal ♀ by red bar ♂.

	Non-crossover class		Crossover class	
	Normal tinged	Bar red	Normal red	Bar tinged
Females	3167	3026	2601	2319
Males	2962	2911	2471	2201

[8] Compiled from the unpublished data of one of my students, Mr. HORACE POWELL.

7. LINKAGE OF THE TWO NEW SEX-LINKED CHARACTERS, BLOOD AND TINGED

All of the evidence presented shows that blood gives the same linkage as tinged when crossed to other sex-linked characters. Since they have been shown to be allelomorphic to the same things they should be allelomorphic to each other. The crucial test is given by crossing the two together.

The blood female mated to the tinged male gave 407 blood-tinged compound daughters and 342 blood sons. There was one tinged male

TABLE 45

F_2 from blood ♀ by tinged ♂.

Number	Blood ♀♀	Blood-tinged compound ♀♀	Blood ♂♂	Tinged ♂♂
1	65	64	70	56
2	62	62	72	44
3	96	105	73	117
4	43	43	34	59
5	115	127	102	99
6	50	48	35	35
7	81	101	68	93
8	113	110	114	93
9	125	128	127	122
10	78	76	62	99
Total	828	864	757	817

probably due to non-disjunction. No red-eyed females occur in the F_1; they are blood-tinged compounds, much lighter than their blood brothers. The compound female is about the color of the eosin female. Four classes of grandchildren are realized in the F_2 generation and no red-eyed flies occurred in a total of 5399 (tables 45 and 46). The blood females can readily be separated from the blood-tinged compounds. The eye does not darken with age as does blood.

TABLE 46

F_2 from blood ♀ by tinged ♂.

Number	♀	♂	First bottles			Second bottles			Third bottles		
			Blood and blood-tinged compound ♀♀	Blood ♂♂	Tinged ♂♂	Blood and blood-tinged compound ♀♀	Blood ♂♂	Tinged ♂♂	Blood and blood-tinged compound ♀♀	Blood ♂♂	Tinged ♂♂
1	5	12	110	51	64	101	60	43	138	63	94
4	9	9	98	33	60	79	51	30	172	71	94
5	9	9	62	33	15	76	49	39	119	70	41
6	10	10				15	10	4	—	—	—
7	60	42	15	7	2	65	30	21	29	12	7
Total			285	124	141	336	200	137	458	216	236

The reciprocal cross, tinged female by the blood male, gave 220 blood-tinged compound daughters and 196 tinged sons. These, when inbred, produced the different classes as recorded in table 47, a total of 2634 flies without the appearance of a red-eyed fly.

TABLE 47

F_2 from tinged ♀ by blood ♂.

Number	Blood-tinged compound ♀♀	Tinged ♀♀	Blood ♂♂	Tinged ♂♂
1	55	69	54	50
2	101	117	102	108
3	84	99	67	87
4	60	74	48	66
5	73	106	106	100
6	121	113	140	116
7	146	152	98	122
Total	640	730	615	649

PART IV. ON THE BEHAVIOR OF THE NEW SEX-LINKED MUTANTS BLOOD AND TINGED WITH A NON-SEX-LINKED MUTANT, PINK. A CONSIDERATION OF MULTIPLE FACTORS

I. CROSSES INVOLVING THE FACTORS p, w^b AND THEIR DOMINANT ALLELOMORPHS P AND W

Comment has already been made upon the resemblance between blood and pink. To one not familiar with these two colors they might readily pass for the same thing. In fact it is impossible at times to separate the two when mixed. Their behavior in heredity however is quite different. STURTEVANT (1913) demonstrated that pink lies in the third chromosome. It is the purpose of this section of the paper to show the effect on eye color when the factors, p, w, w^b, P and W, are brought together in different combinations.

a. *Blood ♀ by pink ♂*

In F_1 there are 794 red females[9] of the wild type and 646 hetero-pink blood males with eyes much lighter than either blood or pink. This lighter color in the blood males is due to dilution caused by the heterozygosity for pink. The F_2 generation from this cross was obtained. Considerable variation in color results from the different factor combinations, as one might expect. The flies were separated into three colors:

TABLE 48

F_2 from cross between the blood ♀ and pink ♂.

Number	pPw^bW XX PPw^bW XX pPw^bW XX	PPw^bw^bXX pPw^bw^bXX pPw^bw^bXX ppw^bWXX	ppw^bw^bXX	pPWXY PPWXY pPWXY	PPw^bXY pPw^bXY pPw^bXY ppW XY	ppw^bXY
	Females			Males		
	Red of wild type	Light red	Very light	Red of wild type	Light red	Very light
1	51 43	52 65	13 14	43 45	50 68	7 7
2	69 33	88 61	20 10	57 32	74 48	21 9
3	42 95	44 127	14 26	31 62	39 126	11 24
Total	333	437	97	270	305	79
Calculated distribution	*324*	*432*	*108*	*246*	*328*	*82*

[9] Plus five very light females (plus one red male?)

(1) Red of the wild type; (2) Flies with eyes almost white; (3) Flies with varying amounts of red. Table 48 gives the flies as distributed to the three different classes. The calculated distribution shows the way in which the total should have been distributed. The writer was not influenced in classifying the flies to meet the demands of the formula, for the experiment was completed several months before the computation was made. The close parallelism that exists between the observed and calculated numbers may be taken as evidence that a correct grouping of the colors has been made.

This experiment was repeated in order to keep under observation the range of colors that results in the F_2 generation. It was evident that some flies appeared whose eyes darkened with age, a condition typical of pink stock. It is evident from the formula that some pinks are demanded. Table 49 records the results of this cross. The grandchildren are divided into four classes: Red eyes of the wild type; dark red eyes corresponding to pink; lighter reds; and flies with eyes almost white. The actual and calculated distribution of the total are in fairly close agreement. In making the calculation the reds were not taken into consideration since no mistake could have been made in their classification.

TABLE 49

F_2 from blood ♀ by pink ♂.

Number	Females				Males			
	Red of wild type	Dark red	Light red	Very light	Red of wild type	Dark red	Light red	Very light
1	24	18	15	11	20	12	11	12
1 a	57	11	49	2	58	3	45	5
1 b	14	2	8	1	10	7	12	2
2	13	3	27	4	11	6	15	0
2 a	44	3	26	3	29	1	30	2
3	20	2	23	8	19	3	12	3
3 a	28	4	35	4	28	6	31	1
3 b	8	0	6	1	5	0	6	1
4	43	9	31	5	45	9	36	5
4 a	95	8	78	6	82	6	70	5
4 b	33	2	16	2	16	5	12	1
5	31	7	33	7	33	6	26	5
5 a	36	3	15	6	27	8	20	4
5 b	0	0	5	1	3	0	5	1
Total	337	50	317	45	332	48	285	30
Calculated distribution	*246*	*82*	*246*	*82*	*219*	*73*	*219*	*73*

b. *Pink ♀ by blood ♂*

All of the F_1, both sons[10] (808) and daughters (847), resulting from this combination have red eyes of the wild type. These when inbred produced the different classes given in Table 50. The F_2 females were classified into two groups, red of the wild type and dark red which is a lighter red than the bright red of the wild fly. There were no homo-pink blood females as in the previous combination and the formula in this case demands none. The table gives three classes of males. I did not calculate the ratios which the formulas demand until after the experiment was completed, and consequently I was not influenced in making the classification. The parallelism that exists between the calculated and observed numbers shows that the grouping of colors and the grouping of the formula are in close agreement.

TABLE 50

F_2 from cross between the pink ♀ and blood ♂.

Number	pPw^{b}WXX pPWWXX pPWWXX PPw^{b}WXX PPWWXX pPw^{b}WXX	ppWWXX ppw^{b}WXX		pPWXY PPWXY pPWXY	PPw^{b}XY pPw^{b}XY pPWXY ppWXY	ppw^{b}XY
	Females			Males		
	Red of wild type	Dark red	Very light	Red of wild type	Light red	Very light
1	176	79	0	88	120	25
2	214	71	0	82	103	20
3	198	62	0	68	111	30
Total	588	212	0	238	334	57
Calculated distribution	*600*	*200*	*0*	*243*	*324*	*81*

In the F_2 of table 50 the formula ppWXY occurs. This would demand that one-fifth of the males, exclusive of the red of the wild type, should be typically pink. In a repetition of this experiment the males were separated into four classes as shown in table 51. The observed and calculated distribution are in close agreement. It would seem from this that the pinks could be separated from the others with a fair degree of certainty.

[10] Plus nine exceptional males with very light eyes.

TABLE 51

F_2 from pink ♀ by blood ♂.

Number	Females		Males			
	Red of wild type	Dark red	Red of wild type	Dark red	Light red	Very light
1	52	10	24	17	17	5
	130	13	63	10	39	2
2	49	15	33	19	14	5
	62	9	38	4	22	2
3	37	6	19	4	11	3
	77	4	35	4	22	2
4	35	9	20	7	22	3
	120	14	57	8	32	11
5	29	6	20	1	20	2
	52	11	27	7	22	7
6	75	20	31	24	12	6
	16	6	6	1	5	2
	97	16	52	7	32	3
Total	831	139	425	113	270	53
Calculated distribution				*87*	*261*	*87*

2. CROSSES INVOLVING THE FACTORS, p, w^b, w^t, AND THEIR DOMINANT NORMAL ALLELOMORPHS, P AND W

a. *Homo-pink blood ♀ by tinged ♂*

The extracted "lights" which result in the F_1 from crossing the blood female to the pink male, are of the formula ppw^bw^bXX and ppw^bXY. They are made by the recombination of the genes of the two recessive mutants and the stock is here designated as homo-pink blood. The expectation is that these flies will breed true. The stock has now been cultivated for more than ten generations. I have seen no less than 10000 of these flies and they breed true to type. These flies are just a shade darker than tinged. In order to measure the value of P as a color factor it was shifted, together with w^b and p, in different combinations by crossing tinged and homo-pink blood stock. Table 52 gives the way in which the different combinations of genes are expected when the homo-pink tinged female is mated to the tinged male. In the F_1 no reds of the wild type are produced. Both sexes however have redder eyes than either parent. The males (244) have darker eyes than

the females (346). This is the expectation since the female is a compound of two members of an allelomorphic system in which a lighter factor (w^t) is involved. Some of the F_1 males are almost as dark red as pink. In the F_2 four classes are produced. The males listed as light are as light as tinged; the light females are of the color of the extracted light; the dark males are darker than the dark females.

TABLE 52

F_2 from cross between the homo-pink blood ♀ and the tinged ♂.

Number	pPw^bw^bXX pPw^bw^bXX PPw^bw^bXX	pPw^bw^tXX PPw^bw^tXX pPw^bw^tXX	ppw^bw^bXX	ppw^tw^tXX	pPw^bXY pPw^bXY pPw^bXY	PPw^tXY pPw^tXY pPw^tXY	ppw^bXY	ppw^tXY
	Females				Males			
	Blood	Blood-tinged compound	Very light and almost white		Blood	Tinged	Very light	Almost white
1	17	15	7	2	14	10	8	2
2	50	37	13	9	43	47	11	14
3	38	40	11	8	27	34	9	7
4	52	37	9	8	36	42	10	11
Total	157	129	40	27	120	133	38	44

TABLE 53

F_2 from cross between the tinged ♀ and homo-pink blood ♂.

Number	pPw^tw^bXX PPw^tw^bXX pPw^tw^bXX	PPw^tw^tXX pPw^tw^tXX pPw^tw^tXX	ppw^bw^tXX	ppw^tw^tXX	pPw^bXY PPw^bXY pPw^bXY	pPw^tXY PPw^tXY pPw^tXY	ppw^bXY	ppw^tXY
	Females				Males			
	Tinged-blood compound	Tinged	Slightly darker than tinged Classed with tinged	Practically white Classed with tinged	Blood	Tinged	Like eosin male	Practically white
1	72	111			56	73	17	19
2	71	140			75	69	22	22
3	57	99			58	52	15	14
4	67	92			44	47	7	11
5	65	104			72	63	12	14
Total	332	546			305	304	73	80

b. *Tinged ♀ by homo-pink blood ♂*

All the sons (102) from this cross are as light as tinged. The females (102) are darker than their brothers. The daughters are of the same color as the F_1 females of the former cross, with which they were directly compared.

Table 53 gives the combinations of the different factors as shifted together in the F_2 generation.

c. *Wild red ♀ by homo-pink blood ♂*

The sons (101) and daughters (91) from this cross have red eyes of the wild type. These when inbred produced in the next generation the classes given in table 54. The parallelism that exists between the expected classes from the analysis and the observed results show beyond question that a correct assignment of genetic formulae has been made.

TABLE 54

F_2 from cross between the wild red ♀ and homo-pink blood ♂.

	PPWWXX pPw^{b}WXX PPw^{b}WXX pPWWXX pPWWXX pPw^{b}WXX	pPw^{b}WXX ppWWXX	PPWXY pPWXY pPWXY	ppWXY	pPw^{b}XY PPw^{b}XY pPw^{b}XY	ppw^{b}XY
	Females		Males			
Number	Red of wild type	Pink	Red of wild type	Pink	Blood	Very light
1	124	37	67	20	52	14
2	131	32	58	14	60	10
3	95	25	52	11	60	9
4	145	35	56	12	67	5
Total	495	129	233	57	239	38

d. *Homo-pink blood ♀ by wild red ♂*

The sons[11] (62) had eyes very much like those of blood stock while the daughters (105) had red eyes of the wild type. These were inbred with the results given in table 55. These classes conform to expectations, as the formulas show.

[11] Plus five red-eyed males of the wild type.

TABLE 55

F_2 from cross between the homo-pink blood ♀ and the wild red ♂.

Number	pPw^bWXX PPw^bWXX pPw^bWXX	ppw^bWXX	pPw^bw^bXX pPw^bw^bXX PPw^bw^bXX	ppw^bw^bXX	$pPWXY$ $PPWXY$ $pPWXY$	$ppWXY$	pPw^bXY pPw^bXY PPw^bXY	ppw^bXY
	Females				Males			
	Red of wild type	Pink	Blood	Very light like eosin ♂	Red of wild type	Pink	Blood	Very light like eosin ♂
1	62	20	40	14	61	25	55	20
2	56	12	29	3	62	18	42	5
3	53	10	35	7	54	19	35	8
Total	171	42	104	24	177	62	132	33

In the preceding experiments we have dealt with the normal gene W and two of its modifications w^t and w^b in their relation to the factor p and its dominant normal allelomorph P. This involves the problem of multiple factors. When both P and W are present the fly is red. If either P or W is present the eye is of a lighter color. If neither P nor W is present the eye is almost white.

CONCLUSIONS

1. This paper records the appearance by mutation of two new recessive sex-linked eye colors from the wild stock of *Drosophila ampelophila*. Tinged, as the name implies, has the least trace of color. Blood is a dull red resembling a dried blood stain. It does not show the brightness of the eye color of the wild stock. Blood may show a marked range of color depending upon cultural conditions. If the cycle of development is short, as happened during the warm summer months, the eye is almost white. The eye darkens to the typical blood as the fly grows older. If development is delayed the eye may be almost typical of blood when the fly emerges from the puparium. Both mutations show typical sex-linked inheritance.

2. When white, tinged, eosin, cherry and blood are crossed with each other, no red-eyed flies appear in either the F_1 or F_2 generation. This fact when taken in connection with the independent origin of the five factors from red, proves that they form a system of multiple allelomorphs.

3. Blood and tinged show the same linkage values with the sex-linked character yellow, and with miniature. These values agree with the recorded linkage values for white, eosin and cherry when crossed with miniature and yellow. These experiments have added the following data upon crossing over.

Loci	Total	Crossovers	Crossover value
y and w	7354	171	2.3
w and m	18254	6716	36.8
w and B'	24059	10703	44.4

4. The conclusions are based on approximately 200000 flies.

5. A mosaic female appeared in the F_1 from a cross between the blood female and eosin male. The right eye was typical of blood, while the left eye was typical of the eosin male. The female was genotypically of the formula $w^e w^b XX$, and since she is a compound she should have had eyes lighter than blood but somewhat darker eyes than the eosin female, as did all of her sisters, with which she was directly compared. The fact is explicable on the assumption that the two X chromosomes became separated after fertilization in such a way that w^b and w^e were carried to the right and left eye respectively. This suggests that the color is due to the chromatin complex elaborated in the cells of the eye itself and is not secondary in the sense that this color is influenced by some secretion given off by the sex glands. This conclusion is in agreement with the results obtained in the case of castration upon insects.

6. The evidence goes to show that the linkage value of factors in the X chromosome does not change with age.

Many of the experiments reported in this paper were carried out simultaneously and verified independently by my students, LENORE McQUINN, A.B., HELENA MAPES, A.B., ADAM BOWLES, A.B., HORACE POWELL, A.B., and RICHARD SIGLER. The care and enthusiasm with which they carried on the work have been a constant source of help and inspiration.

The colored plate (drawing by Miss WALLACE) accompanying the following article (HYDE and POWELL 1916) is an excellent reproduction of the eye colors. T. H. MORGAN, under whose direction the plate was made, has helped in many ways in this study.

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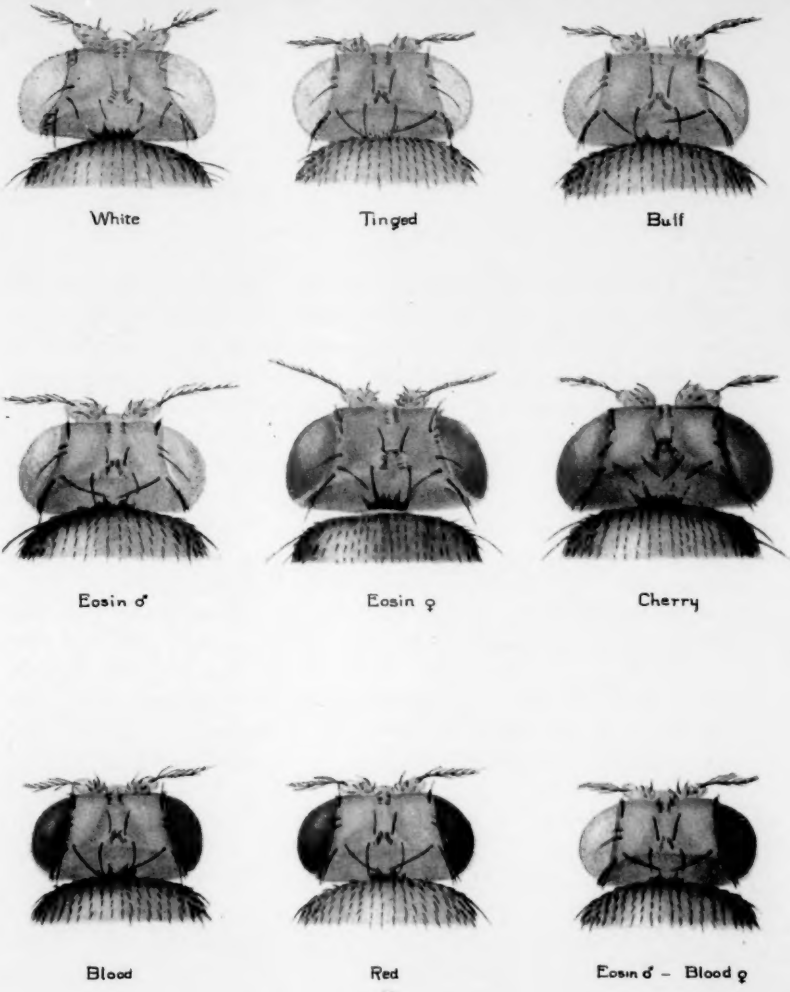

E. M. Wallace, Del

Septuple system of allelomorphs of eye colors, and a bilateral gynandromorph, in *Drosophila ampelophila*.

MOSAICS IN *DROSOPHILA AMPELOPHILA*

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[Received June 6, 1916]

The accompanying plate shows a mosaic female that resulted from a cross between blood and eosin,—two mutant stocks of Drosophila. The right eye of this mosaic was typical of blood stock, the left was typical for males of eosin stock. Neither eye was of the color that characterized some five hundred of her sisters that hatched at the same time. In short the mosaic is a female with two male eyes.

Eosin shows bicolorism,—the eyes of the females are practically twice as red as those of the males. The stock breeds true to this condition. Many experiments carried out with this fly show the genotypical formula of the female to be $w^e w^e XX$, the male $w^e XY$. Blood is a new sex-linked mutation with eyes the color of a blood stain. The senior author has demonstrated that it is a member of the same allelomorphic system as eosin. Many experiments show consistently that the female formula is $w^b w^b XX$ and the male $w^b XY$ (HYDE 1916).

The mosaic female in question appeared in a cross between the blood ♀ and eosin ♂. The females produced by this cross are of the composition $w^e w^b XX$, the males $w^b XY$. This relation is shown by the following diagram:

Eggs from blood ♀,	$w^b X$ — $w^b X$
Sperm from eosin ♂,	$w^e X$ — Y
F_1 flies,	$w^e w^b XX$, $w^b XY$

The females are eosin-blood compound with eyes much lighter than their blood brothers, but considerably darker than eosin females.

The egg that produced this mosaic was of the formula $w^b X$. Since this fly was a female the egg was evidently fertilized by a sperm of the formula $w^e X$. The eyes according to expectation should have been compounds,—lighter than blood but darker than the eyes of the eosin female, as were 500± of her sisters. The fact that one eye was like the eosin male, the other like blood is explicable on the assumption that after fertilization the complex involving $w^e w^b XX$ became separated in

such a way that w^bX was carried to the cells of one eye, producing blood, w^eX being carried to the cells of the other eye, producing the eosin male eye. The result would seem to show that the eye color is not a result of the influence of some substance given off by the sex glands but is due to the chromatin complex carried to the cells of the eye itself.

This fly was under observation for about thirty days. Her eyes were compared many times with her brothers, sisters, eosin stock and blood stock. She proved infertile and no trace of a sex comb or other male characteristic could be found. This case would seem to lend strong support to the view that mosaics may arise through a mitotic disturbance in which the X chromosome is involved.

The second fly was a bilateral gynandromorph that appeared in a cross between the mutant stocks, truncate and white. These stocks had been inbred for many generations and no unusual forms had been found (HYDE 1914).

In a cross between a white-eyed, long-winged male and a red-eyed, truncate female the expectation is red-eyed, long-winged flies in the F_1 generation. Among several hundred offspring from this cross one fly appeared showing both eye colors and a long and a short wing. The white eye and the short wing were on the right side; the red eye and long wing were on the left side;—in short a bilateral gynandromorph, right side male, left side female. The short wing extended slightly beyond the tip of the abdomen and was rounded at the end instead of squared. The short wing in all probability has nothing to do with the truncate condition, but is small, characteristic of the wings of males. The right eye is male, inherited directly from the father through his X chromosome. The white eye has a small fleck of red apparently buried near its center. Two spurs of a sex comb were present on the male side.

The red eye on the left side is obviously female. The long wing would seem to be like the male but in reality its length is characteristically female. Females have larger bodies and correspondingly longer wings than the males. The difference that would result in a bilateral gynandromorph is obvious. We should expect the red eye on the female side of the gynandromorph to be larger than the white eye on the male side. As a matter of fact this eye is considerably smaller. The reduced size of the red eye was probably inherited from the mother since small eyes were characteristic of this truncate stock.

Cases of this kind, as MORGAN (1914) has pointed out, are readily interpreted on the assumption that a mitotic disturbance involving the sex chromosomes occurs in an early cleavage in such a way that the cells on one side of the body get one X chromosome which develops male

characters, those on the other side get two X chromosomes which develop female characters. The fact that a small amount of red occurs in the white eye shows that the disturbance occurred relatively late, possibly during the differentiation of the eye itself. This fly died before her breeding qualities could be determined.

The third mosaic arose from a cross between a red-eyed truncate male and a white-eyed long-winged female. The expectation from this cross is white-eyed, long-winged males and red-eyed, long-winged females. Among the children, however, there appeared a female with both eye colors and both kinds of wings. The white eye and the truncate wing were on the left side; the red eye and the long wing were on the right side. The short wing in this case was a typical truncate wing. The long wing was typical of wild stock with rounded ends. This female was mated to a long-winged white-eyed brother. The offspring were red-eyed long-winged males and females and white-eyed long-winged males and females in approximately equal numbers (table 1). It is to

TABLE 1

Mosaic female by white-eyed brother.

Truncate	Truncate	Red long	White long	Red long	White long
♀♀	♂♂	♀♀	♀♀	♂♂	♂♂
0	0	75	70	65	65

The count as given in this table was not verified by the senior author.

be noted that no truncates appeared in this cross where the expectation is about seven longs to one truncate (HYDE 1914, page 210). With this exception this mosaic female is genotypically the same as her red-eyed sisters which were also tested.

Each side of this mosaic is both maternal and paternal with respect to eyes and wings. The sex chromosomes probably divided normally during the early cleavage stages for had one become separated at this time a gynandromorph would probably have resulted. The appearance of the white and red eye is explicable on the assumption of a later mitotic disturbance involving the X chromosome. No explanation is offered for the wings.

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BUFF, A NEW ALLELOMORPH OF WHITE EYE COLOR IN DROSOPHILA

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In the course of certain experiments to find out the frequency of the occurrence of primary non-disjunction in Drosophila (see BRIDGES 1916), I found a new eye color mutation, "buff" (July 28, 1915), which has proven to be a new allelomorph of white.

Eosin miniature females had been mated to wild males, giving, as expected in the F_1 generation, eosin miniature males and wild type females. But along with these two kinds of flies, there appeared also in one bottle two, and in another eight, females which were long-winged like their normal sisters, but whose eye color was lighter than that of standard eosin females and a little darker than that of eosin males.

These light-eyed females were put into a new bottle where they produced offspring, having evidently been fertilized by their eosin miniature brothers. Unfortunately little attention was paid to the nature of the offspring of the females. Apparently a majority of the sons were eosin with some lighter in eye color. Only one of these males was bred, a miniature male whose eye color was much lighter than eosin, being a pale cream or "buff."

The experiments which are to follow prove that the buff color of this male is a new allelomorph of white. One of the important theoretical questions with respect to a new member of a series of allelomorphs is its origin, whether directly from the wild by a single act of mutation, or indirectly from an already existing mutant member of the series (see MORGAN, STURTEVANT, MULLER and BRIDGES, 1915, Chap. 7). Because of the uncertainty with respect to the offspring of the original light females we cannot be entirely sure in this case whether buff arose from the wild type of the father or from the eosin of the mother. It seems more probable that the buff arose from the wild type of the father for on this view we may explain the light color of the mothers as eosin-buff compound, this light color being without explanation if the buff arose from the eosin.

The buff miniature male was mated to a wild female and gave in the F_1 generation only red daughters (195) and red sons (187) which shows buff to be recessive. About half the F_2 males but none of the F_2 females showed the "buff" color, which is thus shown to be due to a sex-linked gene (table 1). Not one of the sons was eosin in color;

TABLE 1

P_1 wild ♀♀ × buff miniature ♂♂. F_1 wild type ♀♀ × F_1 wild type ♂♂.

	Non-crossover ♂♂		Crossover ♂♂		Total males	Crossovers	Crossover value
F_2 wild type ♀♀	Buff min.	wild type	Buff	min.			
612	172	194	104	94	564	198	35.2

therefore if buff is eosin plus a modifier which reduces the color to a pale cream then this modifier must be very closely linked to eosin. There remained besides this possibility still two other possibilities: buff might be a simple allelomorph of white or might be in another locus altogether.

The amount of crossing over between buff and miniature (35.2 percent) is in agreement with the amount of crossing over between white and miniature, therefore the view that buff occupies the white locus seemed the more probable one. In subsequent generations (table 2) back-cross experiments were run which furnished in both males and females additional linkage data similar to that of the males of table 1.

TABLE 2

Wild type ♀♀ heterozygous for buff and miniature back-crossed to buff miniature ♂♂.

Non-crossovers		Crossovers				Crossover
Buff min.	Wild type	Buff	Min.	Total	Crossovers	values
512	524	284	302	1622	586	36.1

The buff females which appeared in these back-crosses were of identically the same color as the buff males. This is strong evidence against the modifier-view that buff is eosin plus a linked diluter; for of the great number of tested combinations of eosin with other eye colors (including specific diluters of eosin) there has not yet been found a single one in which eosin does not retain its bicolorism, that is, in which the females are not *darker* than the corresponding males.

Between the two remaining possibilities, namely that buff is a simple allelomorph of white, and that buff occupies a locus distinct from white, we are able to decide by finding more accurately the locus of buff. This was done by finding the amount of crossing over between buff and yel-

low (yellow is at the zero point of the X chromosomes). Yellow, buff and miniature were used in the same experiment so that the occurrence of the very small double crossover class might give conclusive evidence as to the location of the genes.

A buff miniature female was mated to a yellow male and yielded in the F_1 generation wild type females and buff miniature males. A few of these were inbred and gave (table 3) in the males the desired linkage information. The yellow buff miniature males were used to run two three-point back-crosses (tables 4 and 5).

TABLE 3

P_1 buff miniature ♀♀ × yellow ♂♂. F_1 wild type ♀ × F_1 buff miniature ♂.

	F_2 females				F_2 males								
	Non-crossovers		Crossovers		y / w^{bf} m		y | w^{bf} m		y / w^{bf} | m		y | w^{bf} | m		Total males
No.	Buff min.	Wild type	Buff	Min.	Yellow	Buff min.	Yellow buff min.	Wild type	Yellow min.	Buff	Yellow buff	Min.	
1	71	58	36	35	57	60	2	3	31	43	—	—	196
2	41	39	26	37	43	29	—	1	20	19	—	—	112
3	39	50	24	22	33	34	1	1	22	17	—	—	108
4	62	64	28	40	43	65	3	1	20	28	—	—	160
5	43	52	19	19	39	46	—	1	25	24	—	—	135
6	34	39	31	22	35	31	1	—	28	22	—	—	117
7	28	48	21	19	33	39	1	1	24	23	—	—	121
8	27	27	14	13	27	24	—	2	13	8	—	—	74
9	44	38	23	30	33	40	1	3	18	24	—	1	120
10	49	62	27	20	39	45	2	—	27	28	—	—	141
Totals	438	477	249	257	382	413	11	13	228	236	0	1	
	915		506		795		24		464		1		1284

TABLE 4

Wild type ♀♀ heterozygous for yellow, buff and miniature [$\frac{y}{w^{bf}\ m}$] back-crossed to yellow buff miniature males.

	y / w^{bf} m		y | w^{bf} m		y / w^{bf} | m		y | w^{bf} | m		
No.	Yellow	Buff min.	Yellow buff min.	Wild type	Yellow min.	Buff	Yellow buff	Min.	Total
1	79	96	3	5	58	59	—	—	300
2	66	88	—	1	41	57	—	—	253
3	56	50	—	1	30	29	—	—	166
4	74	75	2	6	45	54	1	—	257
5	53	48	1	2	29	25	—	—	158
	328	357	6	15	203	224	1	0	
Total	685		21		427		1		1134

TABLE 5

P_1 yellow buff miniature ♀ × wild ♂. F_1 wild type [y w^{bf} m] × F_1 yellow buff min. ♂.

	y w^{bf} m		y | w^{bf} m		y w^{bf} | m		y | w^{bf}	m	
No.	Yellow buff min.	Wild type	Yellow	Buff min.	Yellow buff	Min.	Yellow min.	Buff	Total
1	32	37	3	3	27	24	—	—	
	42	29	1	1	16	19	—	—	
2	39	38	1	—	17	17	—	—	
	32	38	—	—	24	40	—	—	
3	55	56	3	—	19	16	1	—	
	48	45	1	—	29	26	—	1	
4	31	43	—	1	24	17	—	—	
	33	24	1	—	11	22	—	—	
5	45	47	1	2	29	25	—	—	
	60	51	2	—	16	28	—	—	
6	45	53	1	3	18	24	—	—	
	36	35	—	—	22	21	—	—	
7	35	27	1	—	14	16	—	—	
	28	27	—	2	13	17	—	—	
8	22	31	3	1	13	23	—	—	
	30	33	—	1	11	11	—	—	
9	25	44	—	—	18	18	—	—	
	25	29	—	1	9	14	—	—	
10	29	36	1	—	19	15	—	—	
	31	32	—	2	15	19	—	1	
11	38	36	—	3	22	20	—	—	
	52	31	1	1	24	17	—	—	
12	41	53	2	3	25	23	—	—	
	50	46	2	1	24	33	—	—	
13	53	66	2	2	26	26	—	—	
	40	42	1	2	21	21	—	—	
14	71	82	2	1	43	59	—	—	
	71	53	2	1	33	37	—	1	
15	34	33	1	—	16	21	1	—	
	36	37	2	1	15	15	—	—	
16	53	54	1	3	29	40	—	—	
	55	51	1	2	27	33	—	—	
17	38	51	1	2	24	21	—	1	
	34	40	1	1	21	26	—	—	
18	38	30	1	—	31	19	—	—	
	38	43	2	2	19	20	—	—	
19	33	31	1	—	15	22	1	—	
	43	37	2	1	15	15	—	—	
20	31	34	1	1	19	30	—	1	
	38	45	1	—	13	25	—	—	
	1610	1650	46	44	826	935	3	5	
Totals	3260		90		1761		8		5119

TABLE 6

P_1 eosin ♀♀ × buff miniature ♂♂. F_1 eosin-buff ♀ × F_1 eosin ♂.

	F_2 Females		F_2 males					
			Non-crossover ♂		Crossover ♂		Total males	Crossover values
No.	Eosin	Eosin buff	Eosin	Buff min.	Eosin min.	Buff		
1	81	83	66	68	35	43	212	37
2	44	49	50	41	16	20	127	28
3	71	80	46	40	30	18	134	36
4	54	57	26	28	14	19	87	38
Total	261	269	188	177	95	100	560	35

TABLE 7

P_1 white ♀♀ × buff miniature ♂♂. F_1 white-buff ♀ × F_1 white ♂.

	F_2 females		F_2 males					
			Non-crossover ♂		Crossover ♂		Total males	Crossover values
No.	White	White-buff	White	Buff min.	White min.	Buff		
1	53	47	29	25	14	14	82	34
2	65	64	50	35	22	35	142	40
3	45	43	24	32	11	15	82	32
4	52	49	25	31	13	13	82	32
Totals	215	203	128	123	60	77	388	35.3

TABLE 8

P_1 cherry ♀♀ × buff miniature ♂♂. F_1 cherry-buff ♀ × F_1 cherry ♂.

	F_2 females		F_2 males					
			Non-crossover ♂		Crossover ♂		Total males	Crossover values
No.	Cherry	Cherry-buff	Cherry	Buff min.	Cherry min.	Buff		
1	66	65	38	31	20	20	109	34
2	66	76	34	31	10	18	93	30
3	74	75	51	51	35	28	165	38
4	69	65	44	63	30	29	166	38
Totals	275	281	167	176	95	95	533	35.6

By considering the smallest or double crossover classes of tables 3, 4 and 5, it is seen that all the data are consistent with the assumption that the gene for buff lies in the X chromosome between the genes for yellow and miniature, as does white. Furthermore the amount of cross-

TABLE 9

Summary of linkage data.

Genes	Total	Crossovers	Crossover values	Crossover values by MORGAN and BRIDGES
Yellow buff	7537	145	1.9	1.1
Buff min.	14811	5258	35.5	33.2
Yellow min.	7537	2787	36.9	34.3

ing over between yellow and buff is approximately the same as that between yellow and white or any of the other allelomorphs of white.

These linkage experiments limit our possibilities still further; for if buff is due to a gene having no relation to white, then this gene must still be very close to the locus for white, since the linkage relations of buff are practically identical with those of white. The next series of tests effectually proved that the gene for buff must occupy the same locus as white.

The other allelomorphs of white when crossed to each other give intermediates ("compounds") and just such compounds were obtained when a buff miniature male was mated to white, eosin and cherry. In each case the F_1 generation yielded females whose eye color was intermediate between the two eye colors which entered the combination. The white-buff compound was the lightest of the three and the cherry-buff the darkest. No red-eyed flies appeared.

The F_2 from the compounds furnished more compounds in the females, while the male counts showed that the amount of crossing over with miniature is the same for buff as for white, eosin or cherry (tables 6, 7 and 8).

In conclusion, (1) The data have shown that buff is due to a sex-linked gene whose linkage relations are the same as the linkage relations of white (table 9). (2) The occurrence of compounds effectually disposes of the possibility that buff is due to a gene having no other relation to white than a neighboring locus in the chromosome. (3) Against the modifier-of-eosin view we have urged the strong argument of the lack of bicolorism in buff. (4) The linkage experiments have furnished evidence that no modifier could be separated from eosin by crossing over; for in 14251 flies in which such a crossover might have appeared none was found (table 9). (5) We are led then to the conclusion that buff is a simple allelomorph of white. (6) From the evidence upon the

origin of buff it seems more probable that buff arose from the wild than that it arose from the eosin.

My thanks are due to DR. C. B. BRIDGES for his interest in supervising the experiments and in the writing of this paper.

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MUTATIONS IN THREE SPECIES OF DROSOPHILA

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INTRODUCTION

In a preliminary paper (METZ and METZ 1915), two mutations were recorded in *Drosophila tripunctata* Loew., and an undescribed species called "species B." Since that paper was written *D. tripunctata* has been discarded because of its poor breeding qualities, and has been replaced by another species, *Drosophila obscura* Fall., which, together with "species B," has been bred in large numbers during the last eighteen months. In both of these species mutations have occurred within this time. *D. obscura* has given rise to at least three, and "species B" to at least twelve. In addition, an eye color mutant has been found in a third species that was collected for cytological purposes and not bred extensively. Considering all four species together, nineteen mutants have appeared in our cultures.

The most interesting of the mutants, at the present time, are the twelve in "species B,"—or, as I may now call it, *Drosophila virilis* Sturtevant MSS.[1]—because in this species at least three groups of linked factors have already been obtained and it seems probable that more will be evident when all of the twelve factors are tested out. Thus far only

[1] This species is soon to be described by Dr. STURTEVANT, to whom I am indebted for permission to use his manuscript name.

six have been fully tested. Three of these are sex-linked, two others are non-sex-linked and linked together, and the sixth is neither sex-linked nor linked to either of the others. In a subsequent paper I hope to report more fully upon the linkage phenomena when additional factors are studied, and shall here confine myself mainly to a description of the various mutant characters and a brief account of their inheritance.[2]

MUTANTS IN *DROSOPHILA VIRILIS* STURTEVANT MSS.

Normal specimens of this species are dull brown in color with dark red eyes and slightly shaded wings. The males have no sex combs and neither sex has any color pattern on the body save four faint, dark stripes running longitudinally on the dorsal part of the thorax. The mutants, in the order of their appearance, are as follows:

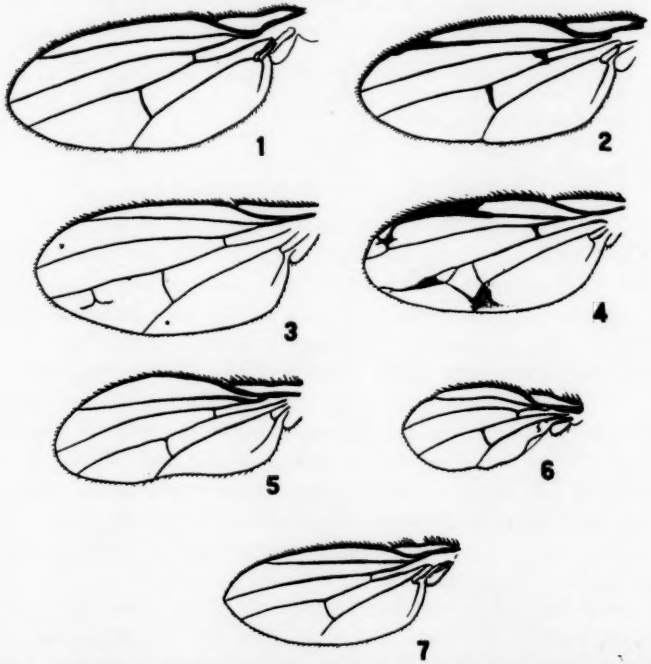

Figure 1. Normal wing of *Drosophila virilis* Sturtevant MSS. Figure 2. Confluent wing. Figure 3. Axillary wing. Figure 4. Confluent axillary wing. Figures 5 and 6. Two types of concave wing. Figure 7. Acute wing.

[2] I am indebted to my wife for making the accompanying drawings, and for other assistance during the course of the work. Acknowledgment is also due to Mr. JOSEPH KRAFKA for aid in the breeding work.

Confluent (figure 2). Non-sex-linked, dominant; wing veins modified. This was described in a previous paper (METZ and METZ 1915).

Axillary (figure 3). Non-sex-linked. Wing veins modified by accessory veins or branches, mostly in the apical half or near the inner margin of the wing; a variable character.

Concave (figures 5 and 6). Non-sex-linked recessive. Wing shape and size modified; one or both wings concave instead of convex on the inner margin, or else reduced in size; hairs on arista curled instead of straight.

Morula. Non-sex-linked recessive. Ommatidia of the eye irregularly crowded together instead of symmetrically arranged in rows.

Yellow. Sex-linked recessive. Entire fly yellow instead of dark brown.

Acute (figure 7). Non-sex-linked recessive. Wing shape and size modified; wings much shorter and narrower than normal, and pointed instead of rounded at the apex; the fifth vein frequently not reaching the margin; anterior pair of orbital bristles often absent.

Steel. Non-sex-linked recessive. An iridescent, metallic, steel-colored spot in the center of the eye.

Bald. Non-sex-linked dominant. Bristles around the ocelli, and frequently the ocelli also, reduced or absent.

Black. Non-sex-linked recessive. Body, legs and wings black instead of dark brown; especially noticeable in the wings.

Glazed. Sex-linked recessive. Eyes with a varnished appearance as if freshly coated with shellac, and with the ommatidia greatly disarranged.

Magenta. Sex-linked recessive. Eye color dark purplish red or magenta, instead of the normal red.

Forked. Sex-linked recessive. Bristles of the head and thorax aborted, twisted and forked, giving a singed appearance.

ORIGIN AND GENETIC BEHAVIOR OF MUTANTS

The first mutant to appear in my cultures of *virilis* was confluent, which arose in July or August, 1914. Its origin and behavior have been described in a previous paper (METZ and METZ 1915), and it is only necessary here to add some further data in support of the conclusion previously expressed, that confluent when present in duplex ("double dose") has a lethal effect. This conclusion was based upon the fact that no homozygous confluent flies could be obtained, and that heterozygous flies when inbred give a ratio of two confluents to one normal, instead of

the expected 3 : 1. Subsequent experiments have borne out this conclusion in every way. Not a single homozygous fly has been found

TABLE 1 a

Confluent by normal.

Culture number	Normal	Confluent
2033	132	110
2122	13	10
2127	10	9
2138	43	36
2148	10	15
2150	45	37
2151	61	42
2156	39	14
2159	50	77
2160	32	26
2170	26	38
2171	19	10
2176	34	30
2178	14	12
2183	29	26
2184	27	12
2185	12	23
2186	14	16
2187	73	47
2201	22	12
2203	28	27
2217	62	47
Total	795	676

TABLE 1 b

Confluent by confluent, from confluent by confluent.

Culture number	Normal	Confluent
1327	21	36
2025	29	50
2024	73	98
2026	43	58
2027	19	23
2028	31	90
2030	44	73
2032	14	36
2048	58	99
2050	33	40
2061	45	61
2105	13	20
2106	8	13
2107	3	7
2108	17	36
2109	32	46
2110	23	63
2111	24	41
2112	20	51
2158	19	47
Total	569	988

TABLE 1 c

Confluent by confluent from confluent by normal.

Culture number	Normal	Confluent
1341	51	74
2072	11	17
2168	20	30
2169	20	26
2174	6	19
V269	52	88
V272	17	23
V277	23	55
V278	16	20
V286	45	76
Total	261	428

among the hundreds I have tested during the two years (over thirty generations) since this mutant appeared. And the ratios have consistently been such as to indicate the absence of the homozygous class in matings of confluent by confluent. Some of these results taken at random from my records are shown in table 1. Three types of matings are given here for comparison: (a) confluent by normal, (b) confluent by confluent, in which the parents are derived from confluent by confluent matings, and (c) confluent by confluent, in which the parents are derived from confluent by normal. According to expectation some of the matings in (a) and (b) should give only confluent offspring while in (c) they should all give three confluents to one normal. In reality no pair has given a purely confluent family; and the ratios in (c) are approximately 2 : 1 instead of 3 : 1. Furthermore the ratios in (b) are just like those in (c), indicating that the parents are alike (heterozygous) in both cases, and that no homozygous flies have appeared. Only one alternative to this explanation occurs to me,—namely, that homozygous flies are produced, but are sterile. This however is made very improbable by the fact that practically all of the confluent flies breed readily and may be tested by mating in pairs.

The second mutant character, axillary, appeared in a normal mass culture during September, 1915. It presents many irregularities both in its manifestations and in its genetic behavior. In pure stock it may vary from a condition in which several extra veins and branches are present in each wing, to one in which only the slightest trace of a branch or extra vein may be seen; or it may be entirely lacking in a portion of the flies. In behavior axillary is usually an irregular recessive, but frequently it shows itself to a slight extent in a few heterozygous individuals. These features are brought out by the data in table 2. It is

TABLE 2 a
Axillary by normal.

Culture number	Axillary	Normal
1378	26	77
2173	19	60
2200	10	66
Total	55	203

TABLE 2 b
Axillary by axillary.

Culture number	Axillary	Normal
2075	10	6
2195	31	29
2212	16	0
Total	57	44

not improbable that axillary depends upon, or is decidedly influenced by, several factors, most of which I have not yet located. Certainly it is greatly affected by at least one factor other than the axillary factor

itself. This factor is confluent. When in the presence of confluent, axillary, instead of behaving as a recessive, becomes an almost complete dominant. This is shown in table 3. When axillary flies are mated to

TABLE 3 a

Confluent by axillary.

Culture number	Confluent axillary	Normal	Confluent	Axillary
2127	6	9	3	1
2170	28	18	10	8
Total	34	27	13	9

TABLE 3 b

Confluent axillary (heterozygous) by normal.

Culture number	Confluent axillary	Normal	Confluent	Axillary
2148	8	10	7	0
2150	22	45	15	0
2151	30	60	12	1
2159	34	77	16	0
2171	4	19	6	0
2176	23	27	7	7
2178	5	12	7	2
2185	13	12	10	0
2186	12	14	4	0
2201	5	22	7	0
2202	2	18	3	0
2203	17	28	10	0
2217	31	60	3	1
2296	18	35	8	1
Total	224	439	115	12

normals they give from five to twenty-five percent of axillary in F_1, and when axillary flies are inbred (pure stock) they give about fifty or sixty percent axillary; but when axillary flies are mated to confluent, or confluent axillary (heterozygous) to normal (it makes no difference which way the cross is made) the percentage of axillary is greatly increased and nearly all of the axillary flies are in the confluent class. Furthermore nearly all of these confluent axillary flies show a greatly exaggerated effect of both confluent and axillary, (compare figures 2 and 3 with figure 4). This peculiar interaction of factors is similar in a general way to many found in *Drosophila ampelophila* and other organisms, except that in the latter, so far as I know, dominance and

recessiveness are not affected (see MORGAN, STURTEVANT, MULLER and BRIDGES 1915, p. 45).

Among the other six non-sex-linked characters five (concave, morula, acute, steel and black) are simple recessives and were each observed in several individuals at their initial appearance. Concave arose in a normal stock culture during September 1915. One concave female from this culture, when mated to normal brothers, gave 64 normal and 17 concave offspring, from which the present stock is descended. Until very recently concave has been looked upon as a variable character, easily affected by the environment, because the characteristic (wing shape) used to distinguish it, was not at all regular in appearance (figures 5 and 6). But I have just discovered that the curled hairs on the arista provide a constant and easily recognizable diagnostic character that will make future experiments relatively simple.

The history of morula is much like the early history of concave. Five morula flies of both sexes appeared in a mass culture and gave rise to the strain now in use. Like axillary, morula sometimes fails to exhibit itself even in homozygous flies, and the ratios are correspondingly distorted (table 4).

TABLE 4

Morula by morula, pure stock.

Culture number	Morula	Normal
1352	52	7
1355	13	0
1356	41	46
1371	130	0
2040	102	25
2044	38	3
2047	14	34
2054	31	1
V11	101	0
V19	6	0
V61	29	5
V69	106	0
V83	48	25
Total	711	146

The character acute appeared in concave stock some time in the early spring of 1916, and was at first thought to be a modification of concave; but when the constancy of this particular type was noticed it was sep-

arated from concave and has subsequently bred true.[3] Aside from the fact that its viability is unusually low it is a typical recessive character.

At about the same time that acute was discovered the eye color mutant steel appeared (February 1916) in a normal stock that had been kept separated from other stocks for several months. Until very recently this character, like concave, was thought to be greatly affected by cultural conditions, but it now appears that exposure to the air, especially warm air, after removal from the moist culture bottle, brings out the character and makes it possible to distinguish a large proportion of the steel individuals.

The mutant black appeared during May 1916 among the offspring of two separate pairs of flies, both derived from a single preceding culture (an axillary by morula cross). In both cases the ratio (approximately 3 : 1) indicates that the parents were heterozygous, and makes it probable that one of the grandparents was pure black. Two black females and one black male from one of the two pairs (number V151) when inbred gave in F_1 ten black offspring and a large number of black-colored pupae that failed to hatch. The ten flies that did hatch were mated together and likewise produced a large number of larvae and pupae but only a few flies, all of which were black. Another culture of three flies, from this same bottle (V151) gave a large number of black flies with abnormal abdomens. These when inbred gave much the same result as the preceding, most of them producing only a few flies from among many pupae. One pair of black flies from the other original bottle (V141) showed a lower degree of mortality among its progeny. It produced 54 offspring (all black) in F_1, and two pairs of these gave 24 offspring in F_2. But stock bottles made up from this are now showing a high degree of mortality similar to that in the other line. Apparently, then, the black factor has a partial lethal effect, or else a lethal factor of some sort is associated with it. Possibly the abnormal abdomen, found in many of the black flies, is an independent character and responsible for the mortality. If so, matings now being made ought to separate the two and give a viable black stock.

The remaining non-sex-linked character, bald, made its appearance in a confluent culture during January 1916. The exact count was not obtained from this bottle, but subsequent breeding has shown bald to be a dominant character, completely or very closely linked with confluent. Unlike confluent, however, it does not always exhibit itself, and the

[3] Other morphological types of concave, such as those shown in figures 5 and 6 have likewise been tested, but are apparently all due to a single factor.

bald class in nearly all matings is unduly small because some of the genetically bald flies appear normal. These features will be considered further under the heading of linkage.

It now remains to consider the four sex-linked characters yellow, glazed, magenta and forked. Yellow has appeared upon two occasions, first (July 1915) in a single male that died without breeding, and second (January 1916) in several males within one mass culture. These latter were successfully bred and gave rise to the present yellow stock. Yellow is a perfectly clear-cut character, breeding absolutely true, and showing typical sex-linkage. Its only peculiarity is its low viability, making it somewhat difficult to breed in pairs. When the original yellow males were mated to normal females they gave in F_1 only normal offspring, and in F_2 165 normal females, 85 normal males and 79 yellow males. When yellow males were mated to heterozygous females they gave normal males and females and yellow males and females in approximately equal numbers. Similarly yellow females mated to normal males gave normal females and yellow males in equal numbers (537 : 544).[4] Additional records involving yellow are given in the section on linkage.

Glazed is a character of recent origin (June 1916) and has not yet been studied extensively. It appeared in one male individual in a mass culture containing steel and normal. When bred to normal-eyed females this male gave in F_1 normal males and females, and in F_2 164 normal females, 85 normal males and 44 glazed males. The F_2 females proved to be of two kinds, as expected,—one homozygous for normal eye, the other heterozygous for glazed. Mated to a normal brother one of the latter gave 36 normal-eyed females, 18 normal-eyed males and 11 glazed males. Another, mated to a glazed male, gave 11 normal females, 17 glazed females, 16 normal males and 9 glazed males.

During the same month in which glazed appeared (June 1916) the character magenta was also found. It arose in acute stock, one pair of which gave 38 normal females, 19 normal males and 17 magenta males. No record was made of the eye color of the parents or grandparents in this case, but it is very probable that the mutation arose with the female used in this mating. Some of the original magenta males were mated to normal females, and others to yellow females. The former gave in F_1 only normal offspring, and in F_2 90 normal females, 43 normal males and 40 magenta males. The latter are considered in the next section

[4] One of these matings gave, in addition, two yellow females and one normal male, apparently due to contamination or non-disjunction.

under linkage. In addition, a number of the normal sisters of the original magenta males were mated to normals, and several gave magenta males in F_1 showing that they were heterozygous for the magenta factor.

The other sex-linked character, forked, appeared in a single male individual (June 1916) from a mating between confluent males and a normal female. When mated to normal females it gave in F_1 only normal offspring, and in F_2 610 normal females, 270 normal males, and 185 forked males. Like most of the other mutants it is less viable than normal, with the result that the mutant class falls below the expected proportion.

LINKAGE

Among the above twelve characters three of the sex-linked and three of the non-sex-linked ones have been tested for linkage. The non-sex-linked characters are confluent, bald, and axillary, of which confluent and bald are closely linked together, while axillary shows no linkage with either. As has been previously noted, bald made its appearance in confluent stock. The bald confluent flies were mated to normals, and *inter se*, with the results shown in table 5. At first it appeared that crossing over took place in one direction, since some of the confluent flies in nearly every case had normal bristles on the head. But when these flies were tested by mating to unrelated normals they all gave bald offspring, showing that the apparent crossovers were due to the failure of bald to exhibit itself. A dozen or more flies were tested in this way and all gave the same results. It will also be noticed that in the table three flies are recorded in the normal wing bald class. These are flies in which one of the four bristles around the ocelli was gone, but the loss of a bristle was evidently purely accidental, for the flies proved to be genetically normal when tested by breeding. Up to the present time no known crossovers have occurred between these two factors.

The results of confluent by axillary matings have already been given in a previous section (table 3), and I need only note here the absence of linkage in this cross. The first four records, and probably several of the others given in table 3, are from matings in which the confluent axillary parents received confluent and axillary from opposite sides, and should, if the characters were linked, give the effects of repulsion, i. e., confluent and axillary should appear mostly in different individuals, seldom in the same individual. Actually, however, the confluent axillary class is larger than the two others combined. Only the assumption of

TABLE 5

Confluent bald (heterozygous) by normal, or inter se, in pairs.

Culture number	Normal head normal wing	Normal head confluent	Bald normal wing	Bald confluent
V133	41	0	1	30
V140	47	22	1	71
V142	36	2	1	52
V143	6	8	0	7
V146	24	2	0	19
V149	33	2	0	36
V167	17	1	0	22
V181	7	0	0	9
V204	15	0	0	14
V206	32	6	0	17
V207	31	14	0	9
V209	33	29	0	13
V210	40	6	0	22
V211	31	24	0	14
V212	41	16	0	15
V220	14	1	0	16
V221	28	5	0	24
V222	34	8	0	15
V223	33	3	0	23
V224	26	6	0	11
V237	50	15	0	11
V242	20	11	0	16
V243	7	3	0	8
V244	25	4	0	10
V247	29	9	0	23
V249	34	11	0	11
V267	21	2	0	15
Total	755	210	3	533

very loose linkage, together with crossing over in both sexes, could explain such a result upon the basis of linkage; and since crossing over in the male has not been demonstrated in this species the assumption is very improbable.

In the group of sex-linked characters it has been possible to ascertain linkage values more rapidly than in the other groups, and three factors have already been located approximately. Or rather, two of them have been located with respect to a third. In both cases the linkage value is low, and the proportion of crossing over high. The first characters tested were yellow and glazed. Unfortunately only two cultures were made up from this cross and the numbers are very small, but in each

case the crossover class is so large as to leave no doubt that the linkage is very loose.

The other characters are yellow and magenta. Males of the latter bred to females of the former gave in F_1 normal females and yellow males. The females bred to normal males gave normal females, and four classes of males in the proportion of 70 brown (body) red (eye), 155 brown magenta, 118 yellow red, and 89 yellow magenta. In this case, as in the former, the linkage is evidently loose, but here it is determined with greater accuracy and the percentage of crossing over may be said to be approximately 36. Or, in the terminology adopted for *Drosophila ampelophila,* yellow and magenta are about 36 units apart.

Knowing the approximate linkage between yellow and glazed, and between yellow and magenta, it may now be predicted that if the factors compose a linear series in this species as they do in *ampelophila* the linkage between glazed and magenta will prove to be either relatively close, if they are both on the same side of yellow, or practically indistinguishable if they are on opposite sides.

COMPARISON BETWEEN MUTANTS IN *D. VIRILIS* AND *D. AMPELOPHILA*

Before turning to the mutants in other species it may be well to consider the relations between those just described and the known mutants in *Drosophila ampelophila.* Some of these relations have been mentioned in an earlier note (METZ 1916) but may be treated more fully here. The first and most striking feature is the apparent correspondence between some of the mutants found in *virilis* and those already known in *ampelophila.* The three characters, confluent, yellow and forked, for instance, are so similar to characters of the same name in *ampelophila* as to suggest at once that they are actual duplicates. In the case of confluent we have three different criteria that point to a correspondence in the two species. First the morphological characteristics, which are practically identical, second the fact that the character is dominant in both cases, and third that it has a lethal effect when the fly is homozygous for it (see BRIDGES 1916). The latter statement must be modified somewhat with respect to *ampelophila,* for confluent flies in that species show a very low viability and many fail to breed. It is possible, therefore, that some of these are homozygous. Likewise the number of offspring produced by confluent flies is so small as to make the ratios questionable; but so far as they go they resemble those in *virilis.* Through the kindness of Professor

MORGAN I secured, some time ago, a stock of confluent *ampelophila* and endeavored to test it out with respect to its lethal effect. The results, from the few pairs that could be induced to breed, are given in table 6. Most of the confluent flies used as parents in these crosses were from confluent by confluent matings and theoretically one third of them should be homozygous. Actually, among the ten flies that bred, only one pair gave purely confluent offspring. Apparently one member at least of this pair was homozygous, unless the result was accidental. Unfortunately no F_2 flies were secured to make certain of the constitution of the F_1, and the evidence is not very conclusive.

TABLE 6

Confluent ampelophila.

a. *Confluent by normal in pairs.*

Culture number	Normal	Confluent
1278	19	13
1285	33	15
1286	45	33
1290	25	24
Total	122	85

b. *Confluent by confluent in pairs.*

Culture number	Normal	Confluent
1288	4	7
1289	2	9
1279	0	27
Total	6	43

These data are meager, but when taken together, and in connection with the fact that in *ampelophila,* as in *virilis,* no homozygous stock of confluent has been secured, it seems probable that the lethal effects as well as other features are similar in both species.

Turning to the two characters yellow and forked, it is to be noted especially that they are both sex-linked in each species. Yellow is slightly darker in *virilis* than in *ampelophila* (see MORGAN 1912), but since the normal *virilis* is much darker than *ampelophila* this is to be expected if the factors really correspond. In the case of forked the morphological correspondence is complete even to the smallest detail, so far as I can tell from a careful comparison of the flies side by side.

So far as the evidence goes, then, it strongly suggests that the factors for confluent, forked and yellow in *virilis* are actually homologous to

those in *ampelophila*. If this is true it follows, as indeed might be expected, that the germ plasms of the two species bear a definite structural resemblance to one another which we may hope to analyze experimentally. Furthermore, if these factors are really homologous, the fact that yellow and forked are sex-linked in each species would indicate that the structural relations of the germ plasm so far as the factorial arrangement is concerned are alike or similar in the two species. And if this is the case it is difficult to avoid the conclusion that there is a genetic continuity of germinal structures—in all probability chromosomes—in these flies.

When the linkage relations between these respective factors are known the evidence will be much more definite; but even if the linkage values are not the same in the two species it does not necessarily mean that the organization is different, for the amount of crossing over might be very different in different species. The crucial test will be to determine whether a linear series similar to that in *ampelophila* is present in *virilis*.

MUTATIONS IN *DROSOPHILA OBSCURA* FALL.

My studies upon *Drosophila obscura* are still in their initial stages and may be passed over with a brief description of the three mutants at hand. The first is characterized by the presence of from one to four extra bristles on the scutellum. It was first observed in October 1915 when several extra bristle flies of both sexes appeared in a mass culture. Subsequent matings have shown it to be a non-sex-linked recessive, but one which is very dependent upon environmental conditions for its manifestation. Table 7 illustrates a typical series of results obtained from homozygous flies mated in pairs. As will be noted some of the pairs give nearly 100 percent of extra bristle offspring, while others give a very much lower percentage. No systematic attempt has been made to determine the agent responsible for these deviations, but it has been noted that in almost every case the higher percentages of extra bristle flies are found in well fed, moist cultures, and the lower percentages in poorly fed, dry cultures.

In the second mutant, triangle, the posterior cross vein forks and forms a triangle at its junction with the fourth vein. This character appeared during February 1916 among the offspring of two separate pairs of flies from a single preceding culture. One of the pairs gave 15 triangle and about 75 normal offspring. The other gave 7 triangle and several normals (exact number not recorded). Two matings of

TABLE 7

Drosophila obscura, extra bristle stock inbred in pairs.

Culture number	Extra bristle	Normal
2191	17	8
021	20	75
022	18	120
029	21	60
030	34	30
031	24	91
032	28	29
033	39	115
034	50	103
037	24	33
038	3	33
040	11	80
041	11	19
049	11	39
051	58	6
052	16	10
057	17	1
061	21	3
Total	423	855

triangle by triangle from these gave respectively 66 triangle: 5 (questionable) normal and 19 triangle: 3 normal. In each case some of the females may have mated with normal males before the cultures were made up,—a fact that may account for the normals in their progeny. Judging from these preliminary data it seems probable that the character will prove to be a simple, true-breeding recessive.

The third mutant is characterized by abnormally short veins in the wing. Both the fourth and fifth veins fail to reach the margin, and occasionally the posterior cross vein is broken. The character is a sex-linked recessive. It appeared during July 1916 in nine males from a mass culture containing extra bristle flies. These males, bred to normal females, gave in F_1 normal males and females, and in F_2 81 normal females, 38 normal males and 38 short vein males. No F_3 flies have been obtained yet, but the character appears to be regular in its behavior.

AN EYE COLOR MUTANT IN *DROSOPHILA SIMILIS* WILL.

Most of the mutants in *Drosophila ampelophila* and in the species just considered, have arisen in more or less highly inbred stock, and it is consequently of interest to note any that have not. Several have already been recorded (HYDE 1915 a, STURTEVANT 1915), and the following is an

additional one. It is distinguished by the possession of chocolate-colored eyes instead of bright red eyes. Flies having this eye color appeared in either the first or second generation of descendants from a normal wild female of *Drosophila similis* that I collected in Cuba. Since the species has never before been bred in captivity there is little chance that inbreeding could have had anything to do with the origin of the mutant in my cultures. The following is a brief history of the character in respect to its origin and behavior: Progeny of a single wild female were transferred without examination, to stock bottles. One of these bottles, examined after the next generation appeared, contained approximately equal numbers of chocolate and red-eyed flies. Three normal females from this, mated to chocolate males, gave 8 chocolate and 7 normal offspring. Five other normal females mated to five chocolate males gave 37 chocolate and 35 normal offspring. Four mass cultures of chocolate flies bred true and gave nothing but chocolate-eyed progeny, (more than 100), as did succeeding cultures of pure stock.

MUTABILITY IN DIFFERENT SPECIES OF DROSOPHILA

In conclusion a word may be said concerning the individual mutative tendencies of the different species of Drosophila thus far studied. The rapid appearance and varied characteristics of mutations in *Drosophila ampelophila* have given rise to the natural impression that this species possesses a peculiar tendency to mutate, not shared by even its close relatives. It is not at all surprising that this opinion has arisen, considering the extraordinary number of mutations obtained from *ampelophila,* but in view of the recent mutations in some of the other species it becomes much less probable that the mutating capacity is peculiar to the one fly. Mutations have now been recorded in six other species,—two in *repleta* (HYDE 1915 a, STURTEVANT 1915), one in *confusa* (HYDE 1915 b), one in *tripunctata* (METZ and METZ 1915), twelve in *virilis* (present paper), three in *obscura* (present paper), and one in *similis* (present paper). These leave no doubt that species other than *ampelophila* have at least some capacity for mutating. Whether this is true of all Drosophilas is, of course, a question; but the fact that mutations have appeared in nearly all the species studied extensively, and in some studied only superficially, tends strongly toward an affirmative answer. In a like manner the evidence furnished by *virilis* and *obscura* tends to modify the conclusions respecting the relative rapidity of mutation in the various species. Of course it is impossible to get more than a rough estimate of the total number of flies examined in any of these species,

but since my cultures of *virilis* alone have given rise to at least a dozen mutations within the last year[5] there can be little question that this species mutates approximately as fast as does *ampelophila*. And in *obscura* the rate can not be greatly different, for here three mutations have already been found among a relatively small number of flies examined.

Taking all of these facts together it seems not improbable that most, if not all, Drosophilas are essentially alike in respect to their tendency to mutate, and that a series of mutations could be found in any of them if sufficiently large numbers of individuals were examined.

[5] Two new ones have appeared since the first part of this paper was written.

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SOME BREEDING PROPERTIES OF THE GENERALIZED MENDELIAN POPULATION[1]

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The generalization of various systems of mating where alternative inheritance occurs has been studied by PEARSON, HARDY, JENNINGS, PEARL and FISH. The most comprehensive study of this subject is presented in the January number of GENETICS by JENNINGS (1916). The fundamental condition of a Mendelian population is there expressed as

(1) $$(G_1)\ r\,AA + s\,Aa + t\,aa$$

A and a represent the dominant and recessive conditions, respectively, of a given character, and r, s and t, integral numbers of individuals of each type. JENNINGS does not derive general expressions for several types of mating whereby G_n can be determined from G_1, hence the purpose of the present paper is to discuss such generalized expressions.

RANDOM MATING

When the mating in G_1 takes place at random JENNINGS shows G_2 to be

(2) $$(G_2)\ (2r+s)^2AA+2(2r+s)(s+2t)Aa+(s+2t)^2aa.$$

He states that the proportions in G_n can be found by applying these two formulas to G_{n-1}, but indicates that the intervening generations must be calculated according to these two formulas in order to determine G_{n-1}.[2]

PEARSON, in 1904, first showed that the F_2 population of a monohybrid cross will produce an F_3 generation having the same proportions of the duplex, simplex and nulliplex types as F_2, providing there is no difference in the fertility of the three types, and that the mating is absolutely at random. This ratio depends on the fact that the two kinds of gametes exist in constant proportions to each other from generation to

[1] Paper No. 4 from the Laboratory of Animal Technology, Kansas Agricultural Experiment Station.

[2] In a correction slip published by Dr. JENNINGS in his reprints of the original article he calls attention to the fact that his formula published in section 8 of his original paper is really general. The writers did not learn of this until after the present paper had been submitted for publication.

generation. Thus when the females of the F_2 population $AA+2Aa+aa$ produce gametes the following results obtain:

AA produces $A + A$ gametes;
Aa produces $A + a$ gametes;
Aa produces $A + a$ gametes; and
aa produces $a + a$ gametes.

These gametes then total $4A + 4a$ gametes or a ratio of one A gamete for each a gamete. But this ratio of $A + a$ gametes holds in the males of F_2 and in the Aa males and females of F_1 as well, hence F_3 shows the same proportions of types as F_2; F_4 as F_3; and so on.

The same condition occurs in the case advanced by JENNINGS. If, for convenience, each individual is assumed to produce only two gametes, G_2 will produce the following proportion of reproductive cells in either sex:
$(2r+s)^2AA$ will produce $(2r+s)^2(A+A)$, or $2(2r+s)^2A$, gametes;
$2(2r+s)(s+2t)Aa$ will yield $2(2r+s)(s+2t)(A+a)$ gametes, or $2(2r+s)(s+2t)A$ gametes and $2(2r+s)(s+2t)a$ gametes;
$(s+2t)^2aa$ will yield $(s+2t)^2(a+a)$ or $2(s+2t)^2a$ gametes.

The total number of gametes produced by G_2 will be

$$[2(2r+s)^2 + 2(2r+s)(s+2t)]A + [2(2r+s)(s+2t) + 2(s+2t)^2]a.$$

Factoring and simplifying this expression the following results are obtained:

$$2\{[(2r+s)^2+2(2r+s)(s+2t)]A + [(2r+s)(s+2t)+(s+2t)^2]a\}$$
$$=2\{(2r+s)(2r+s+s+2t)A+(s+2t)(2r+s+s+2t)a\}$$
$$= 2(2r+2s+2t)[(2r+s)A+(s+2t)a]$$
$$=4(r+s+t)[(2r+s)A+(s+2t)a].$$

Since the factors $4(r+s+t)$ in nowise affect the ratio between A gametes and a gametes, they may be omitted and the ratio becomes

$$(2r+s)A + (s+2t)a$$

But this is the ratio of gametes formed by G_1 in producing G_2, hence G_3 will have the same ratio as G_2; G_4 will have the same as G_3; ad infinitum.

REPRODUCTIVE RATES IN RANDOM MATING

In most Mendelian work the proportions of different types are all that are required, but if a constant rate of mature offspring production is assumed, the inclusion of these constants which were factored out, $4(r+s+t)$, will give the numbers within each group at any subsequent generation. Of course, this result presupposes equal fertility and sur-

vival values for each zygotic group of animals. In G_n the numbers will be, letting m equal the number of mature offspring a female will produce by any one male,

(3) $2^k m^p (r+s+t)^q [(2r+s)^2 AA + 2(2r+s)(s+2t)Aa + (s+2t)^2 aa]$.

The series which k, p, and q will each develop.can be determined by regarding the expression as algebraic, and using the method of the total derivative. If G_2 is differentiated first with respect to A and then with respect to a, if the sum of the partial derivatives is obtained, if the subsequent expression is simplified by factoring, and if the result is multiplied through by m, the constant for rate of reproduction, one will obtain the proportions of gametes produced by G_2. AA and aa will, of course, be treated as A^2 and a^2 respectively. Thus

$$\frac{\partial}{\partial A}[(2r+s)^2 AA + 2(2r+s)(s+2t)Aa + (s+2t)^2 aa] = 2(2r+s)^2 A + 2(2r+s)(s+2t)a.$$

$$\frac{\partial}{\partial a}[(2r+s)^2 AA + 2(2r+s)(s+2t)Aa + (s+2t)^2 aa] = 2(2r+s)(s+2t)A + 2(s+2t)^2 a.$$

Adding, factoring, and multiplying through by m, the gametes produced by G_2 become

$$2^2 m(2r+s)(r+s+t)A + 2^2 m(s+2t)(r+s+t)a.$$

Squaring this expression is equivalent to determining the result of random mating. Factoring the constants from the resulting expression gives G_3 as

(G_3) $2^4 m^2 (r+s+t)^2 [(2r+s)^2 AA + 2(2r+s)(s+2t)Aa + (s+2t)^2 aa]$.

By determining the constant outside of the bracket for a number of generations, k (the exponent of 2) develops the following series, the new term being formed by doubling the old and adding 4:

G_2	G_3	G_4	G_5	G_6	G_7	G_8	G_n
0	4	12	28	60	124	252 - - -	$2^{4(2^{n-3}+2^{n-4} \cdots 2^{n-n})}$

In a similar manner, p (the exponent of m) becomes:

G_2	G_3	G_4	G_5	G_6	G_7	G_8	G_n
2	4	8	16	32	64	128 - - - - -	2^{n-1}

The q series develops the following progression:

G_2	G_3	G_4	G_5	G_6	G_7	G_8	G_n
0	2	6	14	30	62	126 - - - - -	$2^{2(2^{n-3}+2^{n-4} \cdots 2^{n-n})}$

The new term is formed by doubling the old and adding 2, hence any term of the q series is one half the corresponding term of the k series.

In stating these series in general form, n is the number of the genera-

tion in which random mating has taken place. It is apparent that the formula does not apply until n equals 3. For G_1, the original population must be taken, while G_2 is determined by JENNINGS's formula.

It is obvious that these numbers depend on the value of m, but even when m equals 1 the number of individuals will increase so rapidly that not all females will be able to produce offspring by each male. If the mating is perfectly at random this will not affect the proportions of types but it will affect the number of individuals in subsequent generations. If the female can be mated to h males on the average the constant coefficients of $(2r+s)^2AA + 2(2r+s)(s+2t)Aa + (s+2t)^2aa$ become $\frac{h}{r+s+t}$ in G_2, and

$$2^{4(2^{n-3}+2^{n-4}\cdots 2^{n-n})} h^{(n-2)-1} m^{2^{n-1}} (r+s+t)^{2(2^{n-3}+2^{n-4}\cdots 2^{n-n})-2(n-2)+1}$$

in any other generation.

While this gives a general expression for the results of random mating, such mating never occurs, either in nature or under domestication. Some form of selection is always present. The simplest type of selection under domestication is the type to type or assortative mating. JENNINGS has discussed one phase of this, showing that when dominance is involved the groups AA and Aa appear alike, and the G_1 generation of $r\,AA + s\,Aa + t\,aa$ produces in G_2,

$$(2r+s)^2AA + 2s(2r+s)Aa + (s^2+4rt+4st)aa.$$

He finds no general formula by which G_n may be expressed from a knowledge of G_1. The principal pitfall in determining this general expression is involved in keeping the numbers of progeny of each of the different groups in proportion to the number of parents. For example, the progeny of the dominants $r\,AA + s\,Aa$ must be in the ratio of $r+s$ to t, in comparison to the progeny of $t\,aa$. If this precaution is observed the results are readily discovered.

ASSORTATIVE MATING IN THE ABSENCE OF DOMINANCE

Assortative mating may produce two types of results when a single pair of characters are considered, depending on the presence or absence of dominance within the pair. Since the absence of dominance gives rather simpler results it will first be considered. The matings under such a system are:

AA by AA giving AA progeny
Aa by Aa giving $AA+2Aa+aa$ progeny
aa by aa giving aa progeny

It is obvious that, as the generations pass, the homozygous groups will increase at the expense of the heterozygous. The rate at which this takes place depends on the numbers of individuals of each type.

The results of this kind of selection may be expressed in terms of random mating within the group when the proper constants are determined for divisors; or more simply still, the females may be assumed to have a constant rate of reproduction, m, and the ratios for breeding each type may be determined on the basis of m progeny from each mother. Thus $r\,AA$ females in G_1 would produce $mr\,AA$ offspring in G_2; $s\,Aa$ females in G_1 would produce $\frac{ms}{4}\,AA + \frac{2ms}{4}\,Aa + \frac{ms}{4}\,aa$ offspring in G_2; and $t\,aa$ females would produce $mt\,aa$ offspring in G_2. When totalled G_2 would become

$$(G_2)\ \frac{m}{4}\,(4r+s)AA + \frac{2m}{4}\,s\,Aa + \frac{m}{4}\,(s+4t)aa.$$

Since m is a constant that does not affect the ratio, it may be eliminated, and the series G_2 to G_n becomes:

$$(G_2)\ \left(\frac{4r+s}{4}\right)AA + \left(\frac{2s}{4}\right)Aa + \left(\frac{s+4t}{4}\right)aa$$

$$(G_3)\ \left(\frac{8r+3s}{8}\right)AA + \left(\frac{2s}{8}\right)Aa + \left(\frac{3s+8t}{8}\right)aa$$

$$(G_4)\left(\frac{16r+7s}{16}\right)AA + \left(\frac{2s}{16}\right)Aa + \left(\frac{7s+16t}{16}\right)aa$$

$$(4)\ (G_n)\left[\frac{2^n r + (2^{n-1}-1)s}{2^n}\right]AA + \left(\frac{2s}{2^n}\right)Aa + \left[\frac{(2^{n-1}-1)s + 2^n t}{2^n}\right]aa$$

This expression satisfies any values of r, s, and t from 0 up, infinity only being barred because it is incomprehensible in animal breeding. The formula here derived is similar to that obtained by JENNINGS in his section (28), in the case of self fertilization.

ASSORTATIVE MATING IN THE PRESENCE OF DOMINANCE

When dominance is involved there are only two groups to mate on the basis of type, but one group is dizygotic, $r\,AA + s\,Aa$. JENNINGS presents the following proportions in G_2, when G_1 equals $r\,AA + s\,Aa + t\,aa$:

$$(G_2)\ \frac{(2r+s)^2}{4(r+s)\ (r+s+t)}\,AA + \frac{2s\quad(2r+s)}{4(r+s)\ (r+s+t)}\,Aa + \frac{(s^2+4rt+4st)}{4(r+s)\ (r+s+t)}\,aa.$$

Since $4(r+s)(r+s+t)$ is a common denominator that in nowise affects the ratio, it has been omitted in the following calculations. G_1 will produce the following gametes, using the method of total derivatives and adding as previously suggested:

$(r\,AA + s\,Aa)$ will produce $(2r+s)\,A + s\,a$
$(t\,aa)$ will produce $2t\,a$

Squaring these, the result in G_2 becomes

$$(G_2) \quad [(2r+s)^2AA + 2s(2r+s)Aa + s^2aa] + [4t^2\,aa].$$

But $(2r+s)^2AA + 2s(2r+s)Aa + s^2aa$ individuals are the progeny of $r\,AA + s\,Aa$, and $4t^2aa$ are the progeny of $t\,aa$. If the rate of reproduction is alike, then the ratio expressed by the fraction

$$\frac{(2r+s)^2 + 2s(2r+s) + s}{4t^2} \text{ should equal the ratio, } \frac{r+s}{t}.$$

Obviously it does not, hence the equation

$$\frac{c}{d}\,\frac{(2r+s)^2 + 2s(2r+s) + s^2}{4t^2} = \frac{r+s}{t}$$

when solved for c and d gives values which, when substituted should make the two sides of the equation equal. Solving

$$\frac{c}{d}\,\frac{(2r+s)^2 + 2s(2r+s) + s^2}{(4t^2)} = \frac{r+s}{t}$$

$$\frac{c}{d} = \frac{(r+s)\,4t^2}{[(2r+s)+s]^2t} = \frac{(r+s)\,4t}{4(r+s)^2} = \frac{t}{r+s}$$

(G_2) should then equal

$c\,[(2r+s)^2AA + 2s(2r+s)Aa + s^2aa] + d\,[4t^2aa]$, or
$t\,[(2r+s)^2AA + 2s(2r+s)Aa + s^2aa] + (r+s)\,[4t^2aa]$.

This gives the result obtained by JENNINGS, without his denominators

$$(G_2) \quad (2r+s)^2AA + 2s(2r+s)Aa + (s^2+4rt+4st)\,aa$$

Determining the gametes for each subsequent generation by means of the total derivatives already described, squaring, and multiplying by the proper values of $\frac{c}{d}$ for the given generation, which will always equal the inverse ratio of the two groups in the preceding generation, the following develops:

(G_2) $(2r+s)[(2r+s)AA+2s\,Aa] + [s^2+2(2r+2s)t]aa$

$$(G_3)\quad (2r+s)(2r+2s)\,[(2r+2s)AA+2s\,Aa]+[2(2r+2s)s^2+2(2r+2s)\,(2r+3s)t]\,aa$$

$$(G_4)\quad (2r+s)(2r+2s)(2r+3s)[(2r+3s)AA+2s\,Aa]+[3(2r+2s)(2r+3s)s^2+2(2r+2s)(2r+3s)(2r+4s)t]\,aa$$

$$(5)\quad (G_n)\ \prod_{l=1}^{l=n-1}(2r+ls)\{[2r+(n-1)s]AA+2s\,Aa\}+[(n-1)\prod_{l=2}^{l=n-1}(2r+ls)\,s^2+2\prod_{l=2}^{l=n}(2r+ls)t]\,aa.$$

This expression is rather tedious in application, but far less tedious than the determination of the intermediate generations would ever be.

An application of this formula may help to demonstrate its usefulness.

$\prod_{l=1}^{l=n-1}$ indicates a product, where l varies from 1 to $(n-1)$ or $(2r+s)$ $(2r+2s)$ $(2r+3s)$ - - - - - $[2r+(n-1)s]$.

If n equals 5, that is, if the generation under consideration is the fifth in which assortative mating has taken place, the formula would be as follows:

$$(G_5)\ \prod_{l=1}^{l=4}(2r+ls)[(2r+(n-1)s]AA+2sAa]+[4\prod_{l=2}^{l=4}(2r+ls)s^2+\prod_{l=2}^{l=5}(2r+ls)t]aa,$$

or

$$(2r+s)(2r+2s)(2r+3s)(2r+4s)[(2r+4s)AA+2s\,Aa]+[4(2r+2s)(2r+3s)(2r+4s)s^2+2(2r+2s)(2r+3s)(2r+4s)(2r+5s)t]aa.$$

It will be noted that certain of the terms within the parentheses above are common factors. This permits a simplification of the formula, the presence of the common factors showing merely the method of derivation. Omitting these factors the formula becomes:

$$(6)\quad (G_n)\ (2r+s)\{[2r+(n-1)s]AA+2s\,Aa\}+\{(n-1)s^2+2(2r+ns)t\}aa.$$

This is the simplest and most workable expression of the formula. If r equals 3, s equals 2, and t equals 1, this expression becomes in

$$(G_5)\ (6+2)\{[6+(4)2]AA+2(2)Aa\}+\{4(4)+2(6+10)(1)\}aa$$

This equals:

$$8\{14AA+4Aa\}+\{16+32\}aa,\ \text{or}$$
$$16\{7AA+2Aa\}+16\{3aa\},\ \text{or}$$
$$7AA+2Aa+3aa.$$

MATING DOMINANTS ONLY

There yet remains another type of mating, that of dominants alone, which permits of ready generalization. Since the *aa* individuals are dis-

carded, the *AA* type will increase markedly in proportion to the *Aa* type. The *aa* individuals, being discarded, will have no effect on subsequent generations. Since the proportions of gametes are interesting here, their series is introduced as well.

Somatic types	Gametes
(G_1) $r\,AA + s\,AA + t\,aa)$	produces $(2r+s)A + s\,a$
(G_2) $(2r+s)^2AA + 2s(2r+s)Aa + s^2aa$	produces $(2r+2s)A + s\,a$
(G_3) $(2r+2s)^2AA+2s(2r+2s)Aa + s^2aa$	produces $(2r+3s)A + s\,a$
(G_4) $(2r+3s)^2AA + 2s(2r+3s)Aa + s^2aa$	produces $(2r+4s)A + s\,a$
(7) (G_n) $[2r+(n-1)s]^2AA + 2s[2r+(n-1)s]Aa + s^2aa$	produces $(2r+ns)A + s\,a$

If r is given the value 1, and s the value 2, the series mentioned by JENNINGS in his mating (19) results. In F_2 the $AA + 2Aa + aa$ ratio usually occurs, which corresponds to G_1 in the present paper. Using the subscripts of G_1 as in this paper the proportion of individuals in the nth generation becomes

(8) (G_n) (when $r = 1$ and $s = 2$) $(n)^2AA + 2n\,Aa + aa$.

If placed in terms of the ordinary Mendelian symbolism, in F_n the ratio is

(9) $(n-1)^2AA + 2(n-1)Aa + aa$.

The formulas of this paper differ from those of JENNINGS in the method of determining the value of the letter n. JENNINGS lets n equal the number of times the mating has taken place, while the writers have let n represent the number of the generation in which the type of mating has been used. When n equals 1, in JENNINGS's paper, the progeny of the first mating were indicated, while in the present paper, n equals 1 in the generation in which the mating was first practiced. In other words, the writers' nth generation is the parent of JENNINGS's nth generation, or his n equals their $n-1$.

The other types of mating mentioned in JENNINGS's paper already have generalized expressions determined for them.

SUMMARY

Some properties of mating a generalized Mendelian population $r\,AA + s\,Aa + t\,aa$ are considered in this paper; random mating, two types of assortative mating, and mating of dominants alone, being considered. Formulas are presented which will give the proportions of *AA*, *Aa* and *aa*, in any generation resulting from the practice of such matings.

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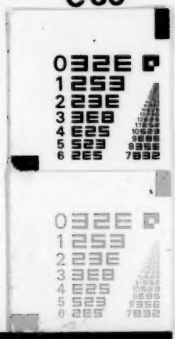
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